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METHODOLOGY AND TECHNIQUES FOR THE STUDY OF ANIMAL SOCIETIES

BY

J. P. SCOTT, JOHN B. CALHOUN, C. R. CARPENTER, N. E. COLLIAS, JOHN T. EMLEN, J. L. FULLER, LEONARD J. GOSS, LAURENCE IRVING, BERNARD F. RIESS, T. C. SCHNEIRLA, AND JOHN W. SCOTT

Consulting Editor
J. P. SCOTT

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Consulting Editor and Conference Chairman
J. P. SCOTT

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*This series of papers is the result of a Conference on *Methodology and Techniques for the Study of Animal Societies*, held jointly by the Section of Biology of the New York Academy of Sciences and The New York Zoological Society on November 12 and 13, 1948.

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FOREWORD

By J. P. Scott

Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

In September 1946, the Roscoe B. Jackson Memorial Laboratory sponsored a conference on genetics and social behavior, which was attended by most of the leading students of animal behavior and animal sociology in this country. One of the important ideas which came out of that conference was the need for the study of animal behavior on the social level of integration, as well as on the individual level, which had been so long emphasized in comparative psychology. This need could only be filled by the study of animals in natural groups, and it implied that greater emphasis should be put on field studies of behavior.

With this purpose in mind, several members of the conference later set up an informal committee for the study of animal societies under natural conditions. The work of the committee was given great impetus by the opportunity afforded it by Fairfield Osborn and the New York Zoological Society to cooperate in setting up a new research center in Jackson Hole, Wyoming, one of the few remaining places in the United States where large numbers of wild animals still live under relatively undisturbed natural conditions. Members of the committee have also worked to promote research opportunities in other places, such as Barro Colorado Island, and have arranged cooperative scientific meetings in which information and ideas could be exchanged between workers in various fields. The first such meeting was held under the combined sponsorship of the American Society of Zoologists and the Ecological Society of America in September, 1948, and the present one, sponsored by The New York Academy of Sciences and the New York Zoological Society, is the second in what is hoped will be a long and useful series. The Jackson Laboratory has cooperated by furnishing the necessary secretarial help to keep the activities of the committee coordinated.

Idealistically, the members of the committee have been motivated by two aims. One is to remedy the deplorable lack of scientific control over destructive social phenomena such as warfare, crime, and poverty. The author has repeatedly stated that it is the duty of every scientist who can do so to help provide the needed information, and that biologists can do their part by providing basic theoretical and experimental material in so far as it can be obtained from animals. The other aim is to promote the conservation of natural resources, which has been strongly advocated by Fairfield Osborn. Particularly in the case of animal species which are threatened with extinction, a vital part of the needed knowledge is concerned with social behavior and organization. One of the paradoxes in this field of knowledge is the fact that highly social species, which are best adapted to thrive under natural conditions, are the first to fall prey to a more highly evolved social system such as that developed by human beings. In any case, the two aims are so closely interrelated that one can hardly be reached without the other.

The prosecution of these aims is obviously dependent upon the further development of an interdisciplinary science which lies between the fields of biology (particularly ecology and physiology) and psychology and sociology. Many names have been given to it, but perhaps the best and most descriptive is "sociobiology."

One of the tasks of any science is to raise and define its standards of work and to agree on common language and uniform standards of measurements, a problem which becomes more important and difficult when the boundaries of traditional disciplines are crossed. The principal purpose of the present meeting was to work toward its solution. It is particularly fitting that The New York Academy of Sciences, which includes all scientific fields, should have been the co-sponsor of the conference with the New York Zoological Society.

In the conference itself, there was, considering the wide diversity of background of the members, a surprising amount of agreement both as to general theoretical approaches and desirable and useful methods. Discussion, for the most part, consisted not in argument but in suggestion of additional points not covered by the formal papers. Attendance was large, indicating that scientists in many formally separate disciplines are independently working toward the same ideas.

It was agreed that the time is not yet ripe for the statement of a set of cut and dried standards for work in sociobiology, a thing which may not be desirable even in the most advanced of sciences. Rather, the papers themselves were of such general uniform excellence that they set a standard to which all workers will have to measure up and, it is hoped, excel in the future.

With this in mind, a review committee, headed by Dr. T. C. Schneirla, suggested that these collected papers could be used as a preliminary handbook for younger workers entering the field. The idea is advanced with humility, and it may be evaluated by describing the contents of the papers.

C. R. Carpenter's paper is an excellent, brief introduction to the subject and particularly emphasizes the need for synthesis in the theoretical realm and the practical problems of planning and administration of research projects.

T. C. Schneirla's paper is a thorough discussion, which relates general scientific theories and methods to the problems and techniques met with in the study of animal behavior. In particular, he points out that the line between laboratory and field work is largely an artificial one, that the techniques and standards of laboratory work can be used in the field, and that in many cases the essential naturalness of the field situation can be preserved in the laboratory.

N. E. Collias's paper, in response to Carpenter's call for synthesis, reviews the general theoretical concepts which have been employed in the field of sociobiology and comes to the conclusion that those ideas are most useful which are based on general and all-inclusive points of view.

There is a whole series of papers which are devoted to the comparative method in sociobiology. That of J. P. Scott emphasizes the need for the systematic collection of facts concerning the basic hereditary behavior patterns in as many species as possible and points out how this knowledge has facilitated understanding of the behavior of certain species and of the problem of domestication in general. The paper by Dr. Riess discusses the criteria by which the roles of heredity and environment interact in determining the basic behavior patterns of any given species, and comes to the conclusion that many of these criteria are not as sound as formerly considered. The paper by J. W. Scott gives an actual example of the results of comparing the social behavior of three related species of birds. One of the interesting points which his paper brings out is the fact that a high degree of social organization is correlated with a smaller amount of fighting. Finally, the paper of John B. Calhoun deals with problems of discovering the optimum environment for different species of animals, based on his own remarkable studies of rats under seminatural conditions.

As a handbook, the group of papers most needs enlargement when it comes to a consideration of special methods. Laurence Irving's paper deals with measuring metabolic reactions to cold, but it is obvious that additional papers could be written on many other physiological activities, including endocrine reactions, as related to behavior. J. L. Fuller's paper deals with one new development in technical apparatus, but there are many others which could be described in a complete handbook. (One of the aims of the committee is to sponsor the improvement and development of apparatus designed for use under natural and field conditions.) To Dr. Goss's paper, on the effects of nutrition and disease in laboratory animals, could be added many special sections on the effects of poor nutrition and parasitism on various kinds of wild animals. J. T. Emlen's paper on the techniques of studying bird behavior could be amplified to include several papers on special methods for mammals, insects, fishes, *etc.*, and the same thing could be said regarding Calhoun's paper on population studies on mammals.

In summary, it may be said that this series of papers may serve as an adequate general introduction to the study of sociobiology and animal behavior under field conditions. It is not, on the other hand, a complete and specialized reference work. The evaluation given above may serve as a rough guide for its use, and, for further facilitation, the summary of each paper may be consulted.

As organizing chairman of the conference, I wish to thank all of those who helped to make the conference a success, particularly Mrs. Eunice Thomas Miner and Dr. Ross Nigrelli of The New York Academy of Sciences, Mr. Fairfield Osborn and his staff of The New York Zoological Society, Doctors R. K. Enders, F. A. Beach, and C. R. Carpenter, who acted as chairmen of the meetings, as well as the authors of the papers. I also wish to extend my regrets to the many competent scientists in the field who either could not attend the conference or could not be asked to give papers because of the limitations of time.

GENERAL PLANS AND METHODOLOGY FOR FIELD STUDIES OF THE NATURALISTIC BEHAVIOR OF ANIMALS

By C. R. Carpenter

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The subject of this monograph and the interests which we represent have closer intellectual kinship with the advanced thinking in the life sciences of the mid-to-late nineteenth century than to the principal currents of contemporary scientific thought. The prevailing "climates of opinions," including scientific value systems and attitudes of the majority of our research colleagues, are of such a character as to impose an unusual burden of proof on us for the professional status of our efforts and achievements. Those of us who are interested in comparative behavior, naturalistic behavior, and interactions of organisms are required to accumulate, and even dramatically to present, an overwhelming weight of evidence on very significant theoretical problems for these areas of research effort to be accepted and duly accredited. Our work is put into a disadvantageous position by the historic flood of poor natural history writing in our fields of interest. At the same time, the prestige of our work is not greatly enhanced by excellent qualitative writings during this quantitative-laboratory age. The question may well be raised: Is the interest and orientation pattern of this monograph archaic or predictive?

Need for Systematic Theoretical Studies. Let us rationalize the need for our efforts to advance the scientific studies of animal adaptations, adjustments, and interactions, and to promote especially the studies of animal groupings living in free-ranging natural conditions.

Perhaps as a reaction against a too broad and diffuse perspective, but also as a consequence of prevailing trends of interpretations of the meanings of science, research methods, and procedures, those approaches have been applied predominantly for purposes of analyses. Analytic procedures have been advanced by the development of suitable apparatus, by needs for strict controls of homogeneous variables, and even by available concepts of mathematics. Seemingly, scientists have been more interested to look inward and to dissect than to look out and to synthesize. Analysis, too, has proven to be easier of accomplishment than synthesis. For example, it is easier to understand the structure and function of a single nerve cell than it is to understand an organism. It is easier to understand an organism than it is to understand a group of organisms. The "law" of least action would seem to apply as a determining factor even to the drift of achievements of scientists.

This monograph may be another indication of a reorientation of efforts and of prospects in the life sciences. Perhaps motivation for reorientation springs from vague awarenesses of the acute and gargantuan problems of social control, social conflict, social integration, and social organization. In contrast to the great need for more certainty of knowledge about social processes is our abysmal ignorance of socio-cultural determinism, of principles and conditions for cooperative group actions, of processes by which values are formed, accepted, and acted upon, and of the role of symbolic processes, myths, and ideologies as determiners of behavior. Perhaps these conditions are motivating us to search for new phylogenetic bases for understanding complex social behavior.

It would seem to be necessary to accept critically and tentatively some of the principles involved in theories of organisms as integrated wholes, but these conceptions are not adequately inclusive. The organism, in turn, is a member of a group, and the group, like the organism, has increasingly complex characteristics. Furthermore, there are requirements to extend our conceptualizations of theories and research to include the organisms and groups in complex environmental envelopes of interdependent processes. For example, Claud Bernard's generalization, which is now known as homeostasis, may be an organizing principle for a range of facts which extend far beyond the *milieu interne* and even to the geophysical and social environments. There would seem to be other organizing principles of equal importance. Can we formulate them?

How shall we best initiate and accomplish our objectives of reformulating and extending current systematic conceptualizations of organismic interactions?

It is proposed that orderly and systematic planning be done on three levels. These levels are: (1) research policies formulation and general overall planning; (2) program planning; and (3) project planning.

Research Policy Planning. There is a very great need for those persons who are charged with the responsibilities for great research and educational institutions to work with all available and summated brain power to establish a strategic framework of research plans and policies. The need is for a diagnosis of the lines of scientific advance, of areas of crucial needs, and of courses of action which have high probability of yielding fundamentally important and useful results. This strategic framework will then give guidance to the efforts of numerous people who will work within the scope of these policies and plans. Institutions, government departments, private foundations, and individuals have as a principal task that of making complex decisions which will effectively channel and orient available (or procurable) human effort, money, and other resources. Without an orientational framework of flexible policies and general plans, all other levels of work are severely handicapped and poorly coordinated.

Program Planning. Program planning is the second level or stage of strategy. On this level, the scope, extent, and objectives of somewhat limited research programs should be reciprocally interactive with formulated general policies. At the level of the research programs, the main tasks are those of formulating theories or testable sets of hypotheses, of selecting and training men, of allocating available resources and of scheduling research operations.

Project Planning. Project planning, the third level, involves all the details of experimental design: the precise statement of the problem to be investigated, the basic and contingent assumptions and postulates, the selection of subjects or organisms (including the important problems of sampling), designing or planning observational procedures, recording, tabulating, summarizing, interpreting, and reporting results.

If we had time to compare this proposed approach with the approaches to field studies which have usually been employed, we would agree that there are marked differences. We may not agree that the differences are advantages. This orderly, systematic, and cooperative approach is suggested as one means and a necessary condition for improving and advancing the studies of naturalistic behavior and of animal societies. The proposal does not and should not allow even the possibilities of prescribed or dictatorial control of individual investigators.

Let there be no mistake, in the scientific courts of appeal, we must expect all evidence, from laboratory and field, to be weighed in the same critical scales and judged by the same criteria. Briefly these criteria are: relevancy, adequacy, reliability, validity, and significance. These will be discussed in more detail by other authors in this monograph.

Especially during our consideration of methods, we should focus our attention on people. The methods, procedures, and techniques are neither better nor worse than the men who use them. Methods and procedures are only tools. Hence, it is of supreme importance to select and train, to high standards, persons who would carry out field studies of animals and their societies. For field workers, there are unusual requirements of background training, breadth of acquaintance with a large number of so-called "branches of learning," and even exacting demands in terms of physical health qualifications. Furthermore, the field worker will often need to "lead and be led in turn" and to work closely and cooperatively with numbers of very different kinds of people.

On the teams of persons and for the kinds of cooperative research in which we are interested, there is no place for the novice, the dilettante scientist, the seeker after raw adventure, the escapist, or the man who has plenty to do with but nothing else to do. Our research teams have difficult requirements to meet and serious work to accomplish. It is our purpose to formulate new conceptual systems and prove them with evidence, to state principles and test them each against other principles, and to record facts in a meaningful context.

In conclusion, here is a list of crucial difficulties and problems of one field worker who would do research on the naturalistic behavior of animal societies:

(1) Lack of a theoretical system which would give meaning and orientation to his observations.

(2) Lack of adequate time, resources, and assistance for completing segments of broadly planned studies.

(3) Lack of entirely satisfactory procedures and specialized field equipment suitable for making and recording observations.

(4) Lack of methods for summarizing and systematizing the numerous variables involved in studies of multiple organisms in geophysical and biotic environments.

(5) Lack of dependable institutional or base support.

(6) Lack of social and professional recognition of the value of results.

THE SOCIAL BEHAVIOR OF DOGS AND WOLVES: AN ILLUSTRATION OF SOCIOBIOLOGICAL SYSTEMATICS

By J. P. Scott

Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine

In any large gathering of present-day scientists, one cannot escape hearing speakers proclaim the need for more scientific knowledge in the field of human relations. Our economic organization broke down and limped along for years during the 1930's, until we became involved in a world war which no one wanted but which no one could prevent. This has impressed even the most isolated and ivory-tower variety of scientist with the fact that man is still able to control his social environment only in the most primitive and unscientific ways.

The author has, in company with a number of other scientists, insisted that a mass scientific attack be made on these problems. As one part of an over-all program, the biologists can give material help by establishing a theoretical science of sociobiology, one of the main subdivisions of which should be the study of comparative sociology of all living species.

However, the sociobiologists should not try to usurp the function of the human sociologists, but rather should try to place human sociology in its proper perspective by comparison with other animal societies and by exploration of experimental situations which would be impossible in human life. In the long run, comparisons of various sorts of animal natures should help to produce a more precise definition of human nature.

Progress in general sociobiology should doubly help to solve social problems arising out of man's poor adjustment to his biological environment, for, as Osborn[9] has pointed out, we cannot have a good human social life without proper conservation of natural resources. We need to know more about human nature in order to get people to help themselves, and more about animal nature so that we can save some of our vanishing species of social animals on which our welfare partly depends.

From the foregoing remarks, it can be seen that even the biologist's part in the over-all plan of a mass scientific attack on social problems is so vast that it requires the cooperation of scientists in many different fields, and the fact that there were gathered at our conference psychologists, ecologists, and geneticists, to mention only a few, demonstrates that this cooperation can be obtained.

The development of this science of sociobiology also requires standardization of techniques and a methodical raising of standards of work. It is, perhaps, too early to be entirely definitive on the score of which methods are essential and which are not. We still need to develop new methods of research, and some of the work to be reported by Irving[6] and Fuller[4] indicates what these developments may be.

On the other hand, we have passed far beyond the stage of the early systematic naturalists, who often observed an animal's behavior, shot the animal so it would not get away, and then speculated upon what it would have done if it had not been shot. Later in this paper, there will be listed several methods of research which appear at the present time to be well founded and indispensable, but only one will be emphasized, as most of the others will be adequately discussed by other authors in this monograph.

The Comparative Method

The particular method to be emphasized has as its theoretical basis the hypothesis that each animal species has characteristic and genetically limited patterns of behavioral adjustment. These patterns do not appear spontaneously but in reaction to particular environmental and internal changes to which they form at least a partial adjustment. [See work of Tinbergen[13] and Lorenz[7] on releasers or primary stimuli.] A paramecium has patterns of behavior which are peculiar to these animals, just as dogs have entirely different patterns which are peculiar to their species. Such patterns of behavior may be suppressed, exaggerated, combined, or associated with secondary stimuli as a result of training, but they remain a limitation which affects the adjustment of an animal to its physical and social environment and which determines, in a large part, the social organization of which it is capable.

This basic behavioral nature of a species is absolutely essential knowledge to a laboratory worker, and to make general conclusions from animal experiments without such knowledge is as foolish as it would be to experiment on human beings without knowing the cultural background of the individual. Yet one can almost count the competent studies of this sort upon the fingers of two hands. Many of these studies have been done by authors of this monograph. The primate studies of Carpenter, the studies of army ants by Schneirla, and that of the sage grouse by J. W. Scott are classics in their field. Among our younger members, many such studies are now being carried on, and we may mention the work of Emlen and Collias on birds and point out that, for the first time, such a study has been made by Calhoun[1] on that popular laboratory animal of the psychologists, the rat.

In comparing the history of sociobiology with that of biology, the newer science appears to be in a Linnaean stage of development. We need accurate descriptions of social behavior in as many species as possible. This means field work, work which is expensive and difficult and which does not always lead to prestige. It is the kind of work that often has to be done by young men without family ties, a fact which I regret, because it sounds like fun. It needs to be done now, for many animal species are almost extinct and others so limited in their distribution that it may never be possible again to obtain a full picture of their social organization.

Since the appearance of various behavior patterns is largely dependent upon the proper environmental situations according to Riess,[10] a great deal more must be done than simply going out and watching the animals and describing their behavior patterns.

Systematic Descriptive Methods

The first step is one of systematic observation of behavior, and there are three main methods of study. The first is the daily round of behavior, which must be studied often enough so that one gets a complete picture of the animal's daily activities. Second, since the environment changes with the seasons, daily behavior must be sampled throughout a complete seasonal cycle. Third, the development of behavior and its changes needs to be studied in an adequate sample of individual animals. Fourth, if possible, these observations should be repeated under a variety of the environmental situations in which the species is found, including various population densities.

These observational data can then be analyzed in a variety of ways, and these analytical methods also serve as a guide for observation. First, the patterns of behavior peculiar to the species should be classified, and, if certain types of patterns appear to be missing, they should be looked for closely. An example of how this may be done will be given in the body of the paper. Second, the social relationships, the composition of groups, and the intergroup relationships should be studied in the manner so well exemplified in Carpenter's studies of primates. Included in this step are, of course, the studies of competition and cooperation emphasized by Collias.[2] Third, and passing into the ecological level, range and territoriality should be considered in relation to social organization. Fourth, important ecological relationships should be studied, including food habits, predator and prey relationships, the effects of parasitic relationships as discussed by Goss,[5] and the climatic limitations of the species, as discussed by Irving.[6]

The special methods which have been used in the case to be reported will now be described. As part of an effort to study individual variability in the social behavior of dogs, it was found absolutely necessary to know the general patterns of behavior in this animal. Since it is a domestic species, it was possible to control to a large extent the ecological relationships of the animal. Food was constant, there was no predation, parasites were eliminated, and climatic conditions were fairly strictly controlled in most cases. Since limiting the environment limits the appearance of patterns of behavior, it was also necessary to make a comparison with field studies of wolves in order to obtain an adequate picture of dog nature. Fortunately, such studies as those of Murie[8] and Young[14] were available.

As one line of study, adult litters of Scotch terriers, fox terriers, and beagles were placed in large one-acre fields and observed while the dogs were unaware of people. Three litters of puppies have been raised by these animals. With the cooperation of visiting workers at the Jackson Laboratory, an intensive study of the daily round of behavior was made during the summer of 1946.* Less intensive observations were made on the same animals throughout a complete season.

As a second line of study, the development of puppies under controlled conditions has been described in detail, including 17 litters of 7 breeds. In addition, occasional observations have been made on some 70 dogs of pure and mixed breeds kept under kennel conditions.

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* The author wishes to thank the following workers and students who assisted in making the observations: C. S. Hall, Benson Ginsburg, J. L. Fuller, Elizabeth Beeman, H. H. Vogel, Jeannie Stewart, Mary-'Vesta Marston, Eleanor Smith, and George Lovell.

Results

The results of the study of basic behavior patterns in large fields were disappointing in three respects. One of these was that certain behavior patterns, such as the male micturition pattern and vomiting by females of food for their young, were almost never seen, although they may be extremely common where dogs are kept in a more varied environment. Another was that there was little evidence of a regular daily round of behavior. Finally, there was comparatively little evidence of social organization in these groups, there being no tendency for any individual to take the lead in allelomimetic activities, and even dominance was seen rather rarely. It was concluded that the only way in which these things could be studied would be to introduce more natural conditions, to let the dogs hunt for their living, come into contact with strange animals, *etc.* Since the space required and the necessary food supply of wild game made this impractical, it was decided that the desired facts could probably only be obtained from field studies on wolves.

Comparison of Dog and Wolf Behavior Patterns

Fortunately there were available three excellent studies of wolf behavior. That of Young and Goldman[14] gives a summary of historical information regarding wolves and of the sort of information which trappers and hunters have collected. That of Murie[8] gives a superb account of wolf behavior under undisturbed natural conditions. Finally, that of Schenkel[11] gives an excellent account of the behavior patterns which wolves develop in captivity in zoological gardens.

After a careful check of these accounts (TABLE 1), it may be said definitely that there is strong evidence that every basic behavior pattern found in dogs is also found in wolves. This means that, in spite of the centuries of selection practiced on dogs, nothing really new in the way of behavior has been developed. This does not gainsay, however, the fact that an extraordinary variability in individual behavior of dogs may be produced by selection and training. It merely means that this variability has been produced by exaggeration or suppression of patterns of behavior already present.

With regard to social organization, it is interesting that there is relatively little evidence of leadership within the wolf pack except as the parents control the immature animals. Hunting often tends to be an individual activity, although the individuals may keep in touch with each other by howling, but daily behavior is organized in a definite round, the animals usually hunting at night and resting in the day time, and there is a seasonal cycle of behavior chiefly organized around reproduction.

In further analyzing these results, it is necessary to consider the basic sensory and motor capacities of the dog and wolf.

Without going into the literature on the subject, it may be stated in general that the olfactory and auditory senses of dogs are unusually good as compared with other mammals, both being apparently better than corresponding senses in man. The visual sense, while relatively good and adapted for both

TABLE 1

COMPARISON OF BEHAVIOR PATTERNS OF DOGS AND WOLVES

Pattern I = infantile pattern only	*Where Reported*	
	Dogs F = Field N = Nursery K = Kennel	*Wolves* M = Murie Y = Young S = Schenkel
1. *Investigative behavior*		
Walking or running with nose to ground, sniffing	F,N	M
Head in air, sniffing, may run from side to side	F	
Sniffing anal and/or genital region	F,N	Y,S
Sniffing nose or face	F,N	M,S
Head raised, ears erect, (listening and looking)	F,N	M
Nosing and sniffing urine or feces	F,N	Y,S
Crawling forward, moving head from side to side, sniffing (I)	N	M?
2. *Epimeletic behavior*		
A. Nest building		
Turning around before lying down	F,N	M
Digging bed in dirt		M
Digging enlargement of den	F	M,Y
B. Grooming		
Scratching self	F,N	
Rubbing against object	F	
Biting own fur	F,N	
Shaking self	F	
Licking own genital or anal region	F,N	
Licking puppies, chiefly in genital and anal regions (eating excreta)	N	Y
C. Feeding		
Allowing puppies to nurse	F,N	
Vomiting food for puppies	N	Y
Carrying food to puppies		M,Y
Food caching (burying food)	N	M
D. Miscellaneous		
Carrying puppies to nest	N	Y
Pushing puppies with nose	N	
Whining (possibly warning)	N	Y
3. *Et-epimeletic behavior* (*attention getting*)		
Whining	F,N	M
Yelping	N	S
Tail wagging (special kinds also seen with agonistic behavior)	F,N	M,Y,S
Licking face (or hands) of person, usually with tail wagging	F,N	S
Touching with paws	N	M
4. *Allelomimetic behavior* (often combined with et-epimeletic, investigative, and agonistic behavior, also)		
Walking or running together	F,N	M
Sitting or lying down together	F,N	M
Getting up together	F,N	M
Sleeping together	F,N	M
Howling in unison	N	M,Y,S
Howling, solitary (loneliness)	N	M,Y

Table 1—*Continued*

Pattern I = infantile pattern only	*Where Reported*	
	Dogs F = Field N = Nursery K = Kennel	*Wolves* M = Murie Y = Young S = Schenkel
5. *Agonistic behavior* (patterns associated with conflict)		
A. Fighting and predation		
Chasing	F	M,Y
Biting	F	M,Y
Snapping teeth	K	Y,S
Pawing	N	
Snarling (showing teeth)	F,N	M,Y,S
Growling	F,N	M,Y
Barking	F,N	M,Y
Wagging tip of tail	K	S
Tail switching		S
Playful fighting, similar to above, but less intense, includes panting	F,N	
Pouncing or springing		M,S
Tossing small game into air		M
Herding	K	M,Y
B. Defense and escape reactions		
Sitting	N	Y
Crouching	F,N	M
Running away	F,N	M
Yelping and showing teeth	N	S
Tail between legs	F,N	Y,S
Rolling on back, pawing and extending legs	F,N	M
C. Attitudes of dominance		
Fore paws on back, growling, tail erect (may bite neck)	F,N	S
Standing over dog on ground, growling	F	
Standing with tail erect	F,N	S
D. Attitudes of subordination		
Allowing dominant animal to place feet on back, tail erect	N	
Tail down	F,N	S
Tail between legs, crouching, ears depressed	N	M?,S
Roll on back, legs extended, tail between legs	N	M,S
E. Miscellaneous		
Hair raising	K	S
6. *Sexual behavior*		
A. Male		
Running with ♀	F	Y
Fore paws extended, body thrown back on haunches, head to one side	F,N	
Licking ♀ genitalia	F,N	S
Mounting	F,N	Y,S
Clasping	F,N	Y?
Pelvic thrusts	F,N	Y?
Copulatory tie	F,N	Y
B. Female		
Running with ♂	F	Y
Forepaws extended, body thrown back on haunches, head to one side	F	M?
Mounting	N	S
Clasping	N	M
Pelvic thrusts	N	
Standing for ♂	F,N	
Tail moved to one side	F	S

TABLE 1—*Concluded*

Pattern I = infantile pattern only	*Where Reported*	
	Dogs F = Field N = Nursery K = Kennel	*Wolves* M = Murie Y = Young S = Schenkel
7. *Eliminative behavior* (see closely related patterns of investigative behavior)		
A. Male		
Micturition with all 4 legs extended (I)	N	
Micturition with lifting of hind leg, usually in places used by other ♂'s	K	S
B. Female		
Micturition in squatting position	F,N	
C. Both sexes		
Defecation	F,N	Y,S
Scratching ground with all four feet following defecation	K,N	Y
Defecation and urination in places previously used	F,N	Y
8. *Ingestive behavior*		
Lapping, tail out and down from body	F,N	Y,S
Chewing and swallowing, same tail position	N	S
Gnawing, holding food with paws	K	
Eating grass	F	M
Sucking, pushing with head, alternately pushing with fore paws, hind feet pushing, tail out and down (I)	N	
9. *Contactual behavior*		
Lying in a heap (I)	N	M
Lying close together	F	M
Curling up	F,N	M
10. *Miscellaneous motor activities not covered above*		
Twitching while asleep (I)	N	
Stretching	F,N	M
Yawning	F,N	M
Rolling over	F,N	M

day and night vision, is not so well developed as in man or some of the birds. The sensory capacities of wolves have, of course, been relatively little explored, but appear to be essentially the same.[14]

If the senses are arranged in a hierarchy of use, it would probably be proper to rank taste immediately after the above three, whereas tactile and thermal sensitivity would rate rather low in the scale.

With regard to motor capacities, the dog is capable of moving the neck and trunk in the limited way characteristic of most mammals. The legs are chiefly capable of flexion and extension in the sagittal plane, and the front legs are capable of a limited amount of adduction. These capabilities are reflected in such activities as crawling, walking, running, jumping, pawing, scratching, digging, clasping, and swimming. There is almost no ability to manipulate objects with the paws, and functions which other species might accomplish in this way are usually done with the jaws, which are used to bite, carry, and pull objects. As with other carnivores, the jaws are not capable of lateral movement, and chewing ability is limited. The tongue is capable of great extension and is used for licking and lapping, as well as a surface of evaporation during panting. Wolves differ from dogs chiefly in being much more powerful in the jaws and legs than most dog breeds.

The ears may be held erect or depressed. The tail may be moved down or up and may be wagged from side to side. The facial muscles are capable of considerable movement during emotional expression, although not so much as in man.

These basic motor capacities can be combined in various ways to produce the more than 50 common behavior patterns seen in dogs and wolves. Comparison was greatly facilitated by classifying these patterns under certain general headings. Such a classification is even more useful for comparing widely different species, since specific behavior patterns may vary so much as not to be identifiable. It also serves as a guide as to what sort of thing to look for in studying behavior of any species. The classification used is essentially that developed in previous papers,[12] and, on the basis of our present knowledge, we can use it to summarize basic dog-wolf behavior patterns in such a way as to give us a general picture.

Investigative Behavior. This is undoubtedly one of the most prominent types of behavior seen in the dog. Even in the samples of behavior in the large pens where real hunting was impossible, investigative patterns of behavior were always the most common. One of the most characteristic activities of dogs is to trot around, investigating objects with the nose and eyes and stopping to look and listen whenever there is a sound.

Allelomimetic Behavior. The tendency to do what the other animal is doing, with consequent coordinated group activity, appears to be fairly strong in dogs, particularly in half-grown puppies. It is principally seen in connection with traveling from place to place or when a common attack is made on prey or a strange dog. Investigation tends to conflict with it in older animals, causing them to separate. The howling of wolves appears to serve chiefly as a device for keeping animals together on a hunt.

Epimeletic Behavior. The giving of care or attention is highly developed in dogs along certain special lines. The tendency toward nest building is rather weak, most animals making use of shelters already provided or enlarging holes already made. Nest building materials are not used. Grooming is likewise rather poorly developed, consisting mostly of the cleaning of very young puppies by the mother. Adults scratch themselves but rarely lick their fur, and there is almost never mutual grooming between adults. Feeding of the young, on the other hand, is highly developed. The mothers not only nurse their young but may vomit food which they have chewed and swallowed themselves. Under the proper feeding conditions, adults of both sexes may provide food for the young and the habit of burying or caching food is frequently seen. This food-providing aspect of epimeletic behavior is therefore highly developed.

Et-Epimeletic Behavior. Attention-seeking behavior is also prominently developed and prolonged from early infancy. The chief patterns are whining and what seems to be a food-begging pattern—wagging the tail, licking the face, and pawing. This sort of approach to adult dogs lasts at least to 4 to 6 months of age, when puppies begin to be less dependent.

Agonistic or Conflict Behavior. As may be expected in a predatory animal, this sort of behavior is prominent, fighting or its alternate pattern of running away occurring rather frequently. Playful fighting is very common in young puppies. There is a tendency to develop dominance under certain conditions, together with characteristic attitudes of dominant and subordinate animals. On the other hand, a well-coordinated group of familiar animals may be strikingly peaceful and cooperative.[8]

Eliminative Behavior. These patterns of behavior appear to have great social significance in dogs, and it is possible that they were originally connected with territoriality. Both sexes have anal scent glands and may scratch the ground after defecation. The micturition pattern differs in males and females. Apparently these reactions are primarily elicited by strange animals.

Sexual Behavior. The dog exhibits two interesting specializations of sexual behavior. One is the comparatively long period of heat in the female, usually including a week or more of preliminary behavior and approximately two weeks of receptivity. The other is the copulatory tie, as a result of which the male and female are attached together. The males can be sexually aroused at any time, but react much more vigorously to specific stimuli from the female in heat.

Ingestive Behavior. There is nothing particularly striking about the ingestive behavior except, perhaps, the tendency toward rapid eating and the ability to go long periods without food or water.

Contactual Behavior. The tendency to maintain bodily contact with other animals is important in young puppies which need it to maintain warmth, but this seems to be relatively unimportant in adult animals.

In conclusion, it may be said that the dogs and wolves show well-developed patterns of behavior under all the major classifications.

Variability of Basic Behavior Patterns in the Dog

At the same time, our studies lead us to believe that the native behavior patterns of the wolf have been importantly modified in the dog in the following ways.

The most obvious of these is, of course, the selection of inherited anatomical peculiarities which make certain behavior patterns difficult or impossible. A dog without a tail cannot wag it and one with lop ears cannot lay them back or hold them erect. Along the same line, certain dog breeds have been selected for specialization in motor capacities, usually at the expense of others. For example, greyhounds can run faster than wolves, but are much weaker in the jaws and their capacity for biting and carrying.

More specifically considered, dogs vary a great deal more than wolves in their investigative behavior, particularly between animals which habitually hunt by scent and those which tend to hunt chiefly by sight and sound. This difference has apparently been accomplished, in the main, by selecting for poor and good olfactory ability.

In connection with allelomimetic behavior, some dogs have apparently been selected to show a much greater attraction and interest in human beings than wolves. Essentially, this means the development of a tendency to respond toward people and dogs in the same way and may have been accomplished by a generalization of the primary stimuli or releasers which bring about this behavior.

Certain breeds appear to have been selected for prolongation of patterns of behavior which originally were typical of young puppies. Et-epimeletic behavior and playful fighting may be extended far into adult life.

With regard to patterns of agonistic behavior, there is wide variability. Selection of patterns of fear and timidity was useful because it is essential in the dog-human relationship that man be dominant. On the other hand, deliberate attempts have been made to exaggerate aggressive patterns of behavior in certain other animals. Dogs, in general, bark more and howl less than wolves, and the tendency to bark varies greatly, from breeds that are very noisy to those which scarcely bark at all.

There is great variability in epimeletic behavior, there being good and poor mothers, and males which are indifferent or solicitous toward young puppies. This variability has apparently been the result of random variation and accidental results of selection for other traits. Decline in these patterns has been possible because the function of epimeletic behavior has been largely taken over by human beings.

There has been a marked change in sexual behavior, inasmuch as female wolves do not mature until two years of age and come into heat only once per year, during the spring months. Female dogs, on the other hand, usually come into heat during the first year, and cycles follow at periods of approximately six months without reference to season. Since at least one breed has been reported to have an annual and seasonal heat period, there is the possibility of exploring an important hereditary endocrine problem here.

Analysis has not proceeded far as to the way in which variability in these behavior patterns has been produced. However, Fuller's work with his reactivity test[3] indicates that animals differ widely in their thresholds of excitability. It is quite possible that this is not a general trait but that an animal may be easily excitable where one behavior trait is involved and difficult to excite in another. This, of course, would almost automatically be true where two patterns of behavior involve conflicting reactions of the autonomic nervous system, and this suggests the hypothesis of hereditary differences in autonomic balance. Fuller has also found that excitability of internal physiological reactions is not necessarily correlated with external reactions.

Fuller's work also indicates that there is a great deal of variability in the ability to inhibit reactions, which appears to be at least partially independent of excitability. In other words, certain animals which are obviously highly active under low levels of stimulation are also easily inhibited by training or restraint. On the other hand, the ability to exhibit restraint may simply be the result of a low threshold for patterns of escape, one manifestation of which is to be quiet. An outwardly calm animal may be either one which is not excited, or one which is easily frightened.

Dogs have, of course, been reported to differ widely in their abilities to learn and to solve problems. Whether or not such abilities exist apart from basic temperamental and social differences as outlined above has not yet been established by our experiments.

Human Behavior and Dog-Wolf Behavior

The comparative method* may also be applied between widely different species and suggests some interesting ideas regarding the process of domestication. Strangely enough, domestication does not seem to have produced anything new in dog behavior. The patterns of behavior of dogs in human society are the same as those of wolves in wolf society. On the other hand, the patterns of behavior in dogs and men are sufficiently similar so that the meaning of dog behavior can, in many cases, be readily recognized by people. The et-epimeletic behavior of babies and puppies is strikingly similar. Nursing in the puppy is similar to nursing in people, and whining and yelping are very similar to crying. The pattern of tail wagging and licking the hands is less familiar, but has been identified with "friendliness" in human beings. The epimeletic behavior in feeding the young is quite similar to that in human beings, and, like human beings, there is a long period of dependency with regard to food. Allelomimetic behavior is similar enough so that dogs and men can walk and travel together. Finally, growling, crouching, and many other forms of agonistic behavior are readily identified by human beings.

Nevertheless, there are certain patterns of behavior which are strikingly different, particularly the female sexual behavior (which may in part account for the unpopularity of female dogs as pets) and eliminative behavior.

As reported by Murie[8] and Young,[14] there are many authentic cases where wolf cubs have been taken away from their parents and made into pets or working animals, and it is difficult to tell these animals from dogs. The evidence from the comparison of human and wolf behavior patterns indicates that the reason for the easy and successful domestication of the wolf lies in the fact that it is a species with highly developed patterns of social behavior and that a large number of these patterns are sufficiently similar to human ones to permit mutual social adjustment between man and the wolf. The primary stimuli are so similar in the two species that appropriate and recognizable social behavior is evoked.

Discussion

The introduction to this paper stresses the need for a mass attack on sociobiological problems by cooperating groups of scientists and, out of the many useful methods now available, emphasizes the need for discovering the basic behavioral nature of as many species as possible. Seen in this light, the observational and comparative material summarized here adds basic information regarding one more mammalian species.

This information is of particular importance because it concerns a species in which there seems to be more variability in basic behavior patterns than in any other species except man, and one which is readily adopted into human society. It lays the groundwork for further experimental work on fundamental theoretical problems of individuality, or personality, as it is often called. Are there such things as individual behavior patterns which always characteristically appear in similar situations, or is the response to each situation different? If such general traits exist, how much are they influenced by heredity and how much by environment? Are there traits which cut across all patterns of behavior or does the generality apply only to special patterns? Given differences in known behavior traits, how do individuals adjust to each other? How do these traits affect performance in social situations? We can now start to answer these questions for at least one species.

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* It should be pointed out here that comparing cannot be done without contrasting, and that differences are just as important as likenesses. Furthermore, the fact that two patterns of behavior can be assigned to the same general class does not imply that they are identical but only that they have some similarity.

From the point of view of methodology, the results described in this paper lead to the conclusion that cooperation is absolutely necessary, that one scientist cannot possibly gather more than a small part of the information required for useful work. From this particular case, it may be concluded that studies of the development of behavior are probably best done under laboratory conditions, where close observation is possible. On the other hand, studies of such things as the daily and seasonal cycles of behavior, social organization, *etc.* are better done under field conditions. Laboratory and field work are almost as mutually necessary as heredity and environment.

The usefulness of the comparative method is borne out, as it leads to some very interesting hypothetical generalizations. One of these is that behavior patterns, like physiological traits, are conservative in evolution and difficult to modify by selection. The other is an interesting idea regarding domestication and social relationships between species in general, namely, that it is based upon a partial similarity in basic behavior patterns.

This, of course, implies that there may be basic limitations on human behavior patterns. In recent years, it has been the fashion, in certain quarters, to say either that human nature is capable of unlimited modifications or that the only factor which modifies it is culture. The only way to check such statements scientifically is by comparing and contrasting animal behavior patterns with human behavior patterns. Bearing in mind the fact that a species which is highly imitative is not nearly so limited in its behavior patterns as some others, we can still say that certain behavioral patterns in the dog, particularly those connected with female sexual behavior and eliminative behavior, are not human behavior patterns and that, while there are probably fewer limitations on human behavior patterns than in most other animal species, they nevertheless do exist.

Summary and Conclusions

(1) The method of studying the basic behavior patterns which are peculiar to a species appears to be one of several which are essential to the complete study of an animal society.

(2) This paper summarizes the results of studying the basic behavior patterns of the dog.

(3) These patterns may be classified under nine principal headings for comparative purposes.

(4) The results of comparisons between dog, wolf, and man lead to the following conclusions.

(*a*) Studies of behavior patterns under both field and laboratory conditions are necessary before any definition of basic behavior traits can be made.

(*b*) Classification of behavior traits provides a useful guide for the study of individual variability in behavior patterns.

(*c*) The principal types of variability seen in dogs are described.

(*d*) This variability has been brought about by exaggeration and suppression of basic behavior patterns rather than by the creation of anything new.

(*e*) Wolves and dogs show certain similarities to human beings in basic behavior patterns, particularly those involved in a long period of dependency of the offspring.

(*f*) It is suggested that a high degree of development of patterns of social behavior, plus considerable similarity in these patterns to those of human beings, is necessary for successful domestication.

(5) In general summary, the evidence and analysis indicates that the wolf is a highly developed social species with many patterns of behavior similar to those of human beings. Consequently, it is easily adopted into human society. The process of selection and random variability have produced hereditary modifications of behavior patterns in dogs which are, at least to a certain extent, comparable to the wide variability of behavior patterns seen in human beings. Training and environmental differences also contribute to this variability, which should be of great use in developing an experimental science of personality.

References

1. Calhoun, J. B. 1950. The study of wild animals under controlled conditions. Annals New York Acad. Sci. **51** (6): 1113–1122.
2. Collias, N. E. 1950. Social life and the individual among vertebrate animals. Annals New York Acad. Sci. **51** (6): 1074–1092.
3. Fuller, J. L. 1948. Individual differences in the reactivity of dogs. Jour. Comp. and Phys. Psych. **41:** 339–347.
4. Fuller, J. L. 1950. Instruments for the measurement of psychological reactions of unrestrained animals. Annals New York Acad. Sci. **51** (6): 1051–1056.
5. Goss, L. J. 1950. Effects of nutrition and diseases on experimental animals. Annals New York Acad. Sci. **51** (6): 1057–1061.
6. Irving, L. 1950. Measurement of some physiological reactions to Arctic conditions. Annals New York Acad. Sci. **51** (6): 1045–1050.
7. Lorenz, K. 1935. Der Kumpan in der Umwelt des Vogels. Der Artgenosse als auslösendes Moment sozialer Verhaltungsweisen. Jour. für Ornith. **83:** 137–213.
8. Murie, A. 1944. The wolves of Mt. McKinley. U.S.D.I. Fauna Series No. 5 Govt. Printing Office. Washington, D. C.
9. Osborn, F. 1948. Our Plundered Planet. Little, Brown and Co. Boston, Mass.
10. Riess, B. F. 1950. Isolation of factors of learning and native behavior in field and laboratory studies. Annals New York Acad. Sci. **51** (6): 1093–1102.
11. Schenkel, R. 1947. Ausdrucks-studien an Wölfen. Behavior, **1:** 81–129.
12. Scott, J. P. 1945. Social behavior, organization and leadership in a small flock of domestic sheep. Comp. Psych. Monograph No. 96, **18** (4): 1–29.
13. Tinbergen, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull. **60:** 6–51.
14. Young, S. P. & E. A. Goldman. 1944. The wolves of North America. Am. Wildlife Institute, Washington, D. C.

THE RELATIONSHIP BETWEEN OBSERVATION AND EXPERIMENTATION IN THE FIELD STUDY OF BEHAVIOR

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The Observer as Investigator

Man goes to nature to learn what nature is, but, in so doing, he introduces possibilities of distortion through his own presence. These risks Bacon had in mind when he stressed the importance of scientific investigation as a means of supplementing and correcting our sense impressions, which are likely to be "infirm and erring."

After a tendency of long standing, observation is frequently viewed as the one necessary field method, and the laboratory is considered the place for experimentation. This view seems justified in part by the fact that field investigation is more obviously dependent, as a rule, upon the worker's immediate perception than is laboratory research. Yet this involves an oversimplification, not only in the sense that the resources of observation as a technique are minimized but also in that the relation of field investigation to the laboratory is misrepresented.

The laboratory holds its place traditionally as the investigative situation in which the scientific study of given phenomena may proceed without the intervention of unknowns of any large magnitude. Unfortunately, this justified emphasis upon laboratory techniques of control has led to the mistaken impression that control may be obtained only under laboratory conditions. This sectarian conception of the "sanctity of the laboratory" has encouraged a narrow view of experimental science, at the expense of the social sciences, in which field procedures are of paramount importance.[10] The difference is not that abrupt. As Warden, Jenkins, and Warner[56] have said, "Obviously, no sharp line can be drawn between careful field observation and simple experimental procedure. In a very proper sense, the laboratory may be considered as a limited and controllable field in which isolation and quantitative measurement of selected aspects of behavior can be made." Properly speaking, in terms of the logic of science, there is really no experimental method as distinct from observation,[59] and the field study of behavior is no exception. A consideration of the advancing scope of experimentation from the physical to the biological to the psychological and social sciences in the present century inevitably broadens our concept of research beyond the scope of the laboratory proper.

Actually, in numerous ways, observation and experimentation are as closely related in field study as they are in other areas of scientific investigation. The role of experimentation in the social sciences, as in science generally, is the refinement of observational techniques.[18] In all scientific research, in field or laboratory, the function of the investigator as an observer of natural phenomena is involved in a variety of ways, which require appropriate control. "Control," in this larger sense, concerns all measures taken to increase the reliability and validity of methods and procedures in a scientific investigation.

In comprehensive studies of individual and social behavior under natural conditions, an effort should be made to advance progressively from a preliminary stage, in which mainly perceptual procedures (such as viewing the animals from a blind) are depended upon, to a stage in which specialized and appropriate manipulative procedures are introduced. The systematic investigator aims at an effective control of conditions throughout, but he learns that this end is achieved in different ways at different stages. From the beginning, any steps taken to facilitate the observer's technique of approach, his mobility and the adequacy of his perception, constitute a regulation of conditions in the phenomenon directed toward promoting reliability and validity of results. Hence all are control measures. From a comparable standpoint, Poincaré[35] appraised the methods of physics, to clarify the observer's influence on the phenomenon he studies through his very intrusion into the situation and his selection of the objects to be studied.[37]

The care taken with preliminary details, from articles of clothing to notebooks and instruments,[13] is designed to introduce the investigator quietly and inconspicuously into contact with the phenomenon, so that he may establish the characteristic nature of the given behavior pattern and its range of variations with dependability. This emphasis upon a maximal intimacy of access to the phenomenon under study brings out a valuable feature of field investigation, in that, first of all, it opens to study and appraisal the entire pattern of the animal's adjustment to its environmental niche-situation. The fundamental precautions directed toward adequacy of preliminary observations thus provide a basis for a later introduction of systematic changes designed to explore what may be termed the inner nature of the phenomenon. The paper of Dr. Emlen will involve a consideration, from this viewpoint, of techniques for the investigation of social behavior in birds.

If scientific methods are means of extending our perception, fundamentally, these means are recognizable in many forms in field work. The assiduous study of terrain, the binoculars and the blinds, living on the study area, and aiming for the fullest expertness of orientation and mobility within it, are such means. Measures of this type are controls in that they reduce the disruptive effect of variables which might be introduced through the intrusion of the observer into the lives of the animals. Such procedures contribute on the one hand to a maximal perception of situation and animals and hence facilitate learning how variations in the phenomenon can be introduced and explored to advantage. On the other hand, they serve to control the "intrusion" factor effectively, provided they are based upon an adequate knowledge of the animal's biological and psychological makeup. For example, the elusive and retiring nature of gibbons in their forest environment was overcome by Carpenter[8] through approach methods and scheduling of operations based upon the typical activities and response tendencies of the animal. Comparably, Nissen[31] designed his approach to chimpanzee groups on such knowledge as the fact that they are chiefly disturbed not so much by human noises and activity in their vicinity as by sudden movements and by "actions which might be effective as directed toward them."

Field work may be thought of as furnishing opportunities for investigation not initially available under laboratory conditions, to be gained through access to the complete natural phenomenon. The two are best considered overlapping and mutually complementary areas of investigation. They are basically similar in method, in that both include perceptual observation in some form as an essential procedure, and the fundamental criteria of reliability and validity of evidence are similarly involved, as are techniques of control through an established basis of understanding and a systematic variation of conditions with reference to this basis. Comparable mental operations are present in both, especially the use of hypothesis, analysis, and synthesis and theorizing in gathering and interpreting results. A common body of problems is studied, although in somewhat different ways.

The field investigator must never be considered simply a "watcher," even when the results of his observations are gathered and reported in a most naïve and uncontrolled form. He is always a perceiver, who is, as Woodworth[60] notes, "not an unbiased registering instrument." As a perceiver, he makes some attempt to interpret what he views, and often his degree of assurance has no relation to whether his acuity and understanding are quite inadequate or are close to the scientific ideal of reliability and validity in these respects. These matters differ, of course, with his sensitivity, intelligence, and personal make-up, his general and special training, his interest in problem and animal, and his bias or expectation of a particular outcome.

About intelligence, we may be hopeful. The other characteristics require further consideration. In the first place, the effective perception and report of meaningful situations is a technique which benefits from systematic training. It is not surprising that in a test by Raymond Pearl,[33] fifteen professional men and scientists, all very interested in genetics, disagreed widely in their results from the sorting of 532 grains of stock and hybrid corn in two characters only, color and form. Obviously, personal differences in acuity, perception, training, and judgment contributed to the outcome. From this, the inference should not be drawn that, in studying behavior under natural conditions, we must resort to a mechanical collection of data which will exclude all personality factors. For one thing, investigators must plan any such procedures in view of their approach to the problem and understanding of it. Then, also, whatever sampling procedures are used cannot be random but must be selective, because behavior phenomena in the wild are not indiscriminate and random but are characteristically systematic and ordered in time and space, with characteristic types of variability.[19] However excellent the mechanical facilities may be, their use must be planned and applied by the intervention of perceiving and thinking individuals.

With reasonably good qualifications at the start as concerns sensitivity, intelligence, and motivation in particular, the observer's technique as a skilled perceiver, reasoner, and manipulator of his subject matter may be advanced through experience to a high degree of scientific reliability and control. The point is emphasized by W. H. Hudson[22] in his comparison of gambler and naturalist: the former able to distinguish readily the most minute differences on the engraved backs of playing cards but quite unable to discern differences in the appearance and behavior of species of common birds, differences readily apparent to the naturalist, who on his part finds the cards all alike on their reverse sides. Some ways in which an improvement in field perception may come about are suggested in Darling's[13] discussion of observational techniques, based on his classical study of group behavior in the red deer of Scotland:

"It takes time for the eye to become accustomed to recognize differences, and, once that has occurred, the nature of the differences has to be defined in the mind by careful self-interrogation if the matter is to be set down on paper. . . . The fact remains that an observer has to go through a period of conditioning of a most subtle kind. . . . [He] must empty his mind and be receptive only to the deer and the signs of the country. . . . This is quite severe discipline, calling for time and practice. . . . It is necessary intellectually to soak in the environmental complex of the animal to be studied until we have a facility with it which keeps us, as it were, one move ahead. We must become intimate with the animal. . . . In this state the observer learns more than he realizes."

A cardinal point is that the observer must consider the single observation only a small part of his task, to be repeated, enlarged upon, and varied as a matter of necessary control. As Carpenter[8] puts it: "The reliability and completeness of the first observation of any given activity can always be increased by repeated checking." That this is a question of the validity of sampling procedures, and not simply one of piling up data, is emphasized by Fisher's[15] statement: "The salutary habit of repeating important experiments, or of carrying out original observations in replicate, shows a tacit approach to the fact that the object of our study is not the individual result, but the population of possibilities of which we do our best to make the experiments representative."

To facilitate the development of observational skills, the observer checks his perception of groupings of animals and of details in their relations to given situations, repeating his work systematically at frequent intervals, to promote his discernment of similarities and of differences according to time and place. He sets out to predict variations in the phenomenon according to known or suspected conditions, noting his predictions so that they may be checked against what actually occurs. Beyond increasing the reliability and validity of perceptual data, such procedures should lead into a progressive experimentalistic approach to the phenomenon.

*Observational Control through Record-Taking**

Adequate techniques in taking records establish a firm basis for minimizing perceptual and mnemonic errors. One must record as he watches events, keeping his eyes and ears on the animals and setting down notes with tactual control as far as possible, in order not to lose "visual touch" with occurrences. Much practice at writing in the dark helps improve the mechanics of this process, and also anticipates inevitable needs in night-time observation. The habit of taking records at all times, regardless of inconveniences such as rain, eliminates lapses of time between perception and statement and stimulates watchful attention to events and their relationships in time. Through such procedures, the investigator becomes a dynamic perceiver of his phenomenon, a "participant" rather than merely a "spectator," in Heidbreder's[20] sense. Qualitative accuracy in note-taking is thereby promoted, rather than mere quantity.

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* Experts who find any of this material somewhat tediously familiar are advised to skip as may seem desirable, provided they do not skip the main point.

Because the processes of organization and interpretation begin with the initial perception and notation of occurrences, good notes inevitably assist methodology at all stages from observation to explanation. The first aim is an adequately complete and accurate report made at the time of occurrence, containing all essentials from routine information (such as date, time, weather, special and general nature of situation) to unusual or specialized matters.* Adequate field notes are stated in a connected and organized manner, following a standard form when appropriate. Usual patterns of events should be noted, not taken for granted and omitted, or variations and exceptions, and opportunities for special tests, will be passed over. An appropriate system of symbols should be devised for representing important aspects of the phenomenon, to promote organization, scope, and depth in the survey.†

For many types of work, a full use of shorthand or speed-writing is almost mandatory. On-the-spot illustrations, such as an outline sketch of a behavioral situation, or some appropriate form of graph which indicates the essential nature of change in a situation, become useful assets when developed systematically. Opportunities for new ways of quantifying records should be sought, from measurements of spatial dimensions to the calibration of important behavioral characteristics. Frequent practice in the estimation of distances is desirable, as in other matters, such as counting animals in groups, judging their spatial arrangement, and so on. Emphasis upon improving and polishing such techniques not only saves valuable time but also stimulates the development of an investigative attitude. Speculative or interpretive comments should be marked distinctively in the notes.

Notes should not be permitted to "rest" once they are in the record books. Each day's notes should be summarized and critically reviewed before one retires for the night. At intervals of a few days, more inclusive surveys of notes should be made, directed not only toward general analytical study, but also toward catching discrepancies, omissions, and latent meanings and otherwise checking the adequacy of the record. Any changes, additions, or deletions which are made in the original notes, at any time after the original observation, should be marked distinctively. These and comparable procedures aid accuracy in perception and record, as well as insight in the planning of further work.

It is assumed that the notes will be supplemented instrumentally whenever appropriate or feasible, through the use of still and motion-picture photography, sound recorders, activity recorders, and the like, with the precaution that such measures shall not displace essential perceptual observations. It is clear that photographic records, opportunely made, have value for subsequent study of the phenomenon in various ways, such as inspecting the scene for overlooked details, quantifying various aspects of behavior, and so on. Sound-recording procedures have possibilities not only for later analysis of the records, but also for experimental use in playing them back to the animals under selected conditions in the field. In fundamental and original studies, however, such records should be considered as secondary and supplementary to the written and graphic notes from observation.

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* In Shelford's[49] basic work on ecological methodology the importance of a thoroughgoing ecological and behavioral coverage in notes is explored.

† For example, in his field study of chimpanzee behavior, Nissen[31] devised convenient symbols for discernibly different sounds he was able to identify according to situation of arousal. Thus "FP" designated "fear or pain situation," and "TT" a situation of general excitement. In part, this system aided the investigator to differentiate the organic and external conditions under which different sounds occurred.

In each field project, an adequate account of the typical daily march of events is essential, as a basis for studies on variations, and to assist the planning of specialized surveys and tests. Such accounts of the daily routine are comparable to laboratory protocols. It is well to bear in mind that even original notes on field events are not to be regarded as mere catalogues of occurrences, but as perceptual accounts which invariably include some interpretation as well. If this fact is taken into account, it can be controlled appropriately. The well-schooled field investigator sets down his hypotheses as clearly as possible in advance, then records his perceived events with an attempt to distinguish what is focal and what peripheral under the conditions, significant variations and their conditions, and discernible relationships. Frequently, the records will include on-the-spot comparisons with other situations, and features worth following up comparatively will be noted. An emphasis upon newly revealed features and relationships makes for a progression and development from one situation to another, and assists the investigator to enlarge his understanding as well as his data concerning the phenomenon.

Specifically, these practices may be regarded as elementary controls guarding against the types of errors made under the conditions of so-called "observational memory" reports, in which results are reported or set down after an interval of time has elapsed. (From studies such as those of Bartlett[3] on this type of report, we may expect the perceiving, thinking, and remembering of observers who attempt to recall their material with inadequate records or without notes to be sprinkled liberally with subtle or gross errors, such as the inclusion of outside material, omissions, and alterations generally dependent upon personal motivation and attitude.) Emphasis upon note-taking techniques also increases adequacy of initial perception. Because observational memory is notoriously low in reliability and in validity, training in the technique of perceiving and emphasis upon adequate record-taking are imperative for control in field observation.

"Personal Equation" in Field Investigation

Because natural phenomena are not random aggregates but are found to be organized, in some respect, in all cases, systematic and controlled methods of selecting cases and collecting data must be found. The field study of social behavior in animals is not unlike that in opinion-poll and survey investigations on the human level, in that the methods cannot be directly transferred from the laboratory but must be developed through study of conditions in the respective field situations. Selected questions considered important must be investigated in (*i.e.*, put to) groups considered representative of their populations. How the operations of selection are carried out is crucial for the adequacy of the study.

These considerations make the psychology of the investigator a matter of importance. The fact that different observers often obtain very different results from what is objectively the same phenomenon emphasizes the existence of individual differences in the psychological factors underlying perception and report, a condition known since 1795 as "personal equation."[5] Toward the control of such matters, we may bring an adequate training in the techniques of approach, of perceptual observation, of record-taking, and of logical processes. Such techniques are, to some extent, general but, in specific detail, must be developed appropriately on an empirical basis for each type of problem.

Obviously, the use of methods supplementing general observation is dependent upon the observer's psychology, in view of the fact that he must select the times and places at which to use particular instruments, according to his conception of the phenomenon and the relative importance of events in it. With sufficient cameras and sound pick-ups, he might conceivably get a fairly complete record of visual and auditory aspects. However, the general worth of the record would depend upon the skill and insight with which the recorders were placed, and finally the task of editing and interpretation would remain to tax his perceptual processes and judgment. Thus, whether or not the use of supplementary mechanical devices aids over-all control is a matter dependent upon the observer, and in particular upon his attitudes toward the subject matter.*

It is evident that in studies of social behavior, our attitudes toward the nature, origin, and relationship of competition, cooperation, and natural-selection processes exert subtle influences not readily controlled in the planning and prosecution of investigations. For example, if our investigations are initiated on the hypothesis that a peck-order conception of social organization is adequate, some inertia is to be expected in our attention to other possible factors in social organization.† The nature of the effective "whole" that is investigated in a given problem depends upon factors of attitude. Whether in field or laboratory, the experimenter's responsibility for control involves the regulation of such matters, and not only the manipulation of objective factors in the phenomenon under study.

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* In the light of recent critiques of the subject (*e.g.*, Sherif and Cantril[50]), we may define attitude as an established and relatively enduring readiness to think and react in given selective ways with respect to objects or situations, under the influence of varying affective and motivational aspects of personality, which owes its characteristic pattern to current situations interactive with the influence of learning and social experience.

† The available evidence suggests that cooperation and competition may have different biological bases in social behavior, and may differ in the degree and nature of their relationship according to phyletic level and environmental conditions.[1, 45]

Observation-Selective and Direct-Manipulative Controls

Field study involves a variety of ways of regulating factors in the phenomenon under study. These may be differentiated roughly as *observation-selective controls* (including procedures of regulating approach, selective techniques in observation, and selection of variations for study) and *direct-manipulative controls* (which are more or less similar qualitatively to regular laboratory controls). All observational investigation involves the first type of control. The relative prominence of the second type depends upon the nature of problem and subject. We have been discussing observation-selective types of control, principally. Now we may turn to a discussion of a class of field problem in which the second type of control holds a prominent place.

Investigations on the problem of ant orientation, used here to illustrate use of direct-manipulative controls in field work, have the longest history of any systematic experimentation upon a behavior problem. They began in 1745, when Bonnet extended his observations on ant columns by the simple "finger test."* Merely rubbing a finger across the route disrupted travel in the column, suggesting the presence of a chemical trail. From that time, research on the way-finding of ants has developed through a long series of investigations, to which Huber, Lubbock, Forel, and Brun[6] have been notable contributors. Since Lubbock, much of the work, particularly that of Brun, has been performed in field and laboratory in a coordinated way. For example, following preliminary observations and tests, the factor of light-compass orientation (*i.e.*, a reaction to direction of light) was postulated, and Santschi developed his "mirror test" to investigate it in the field. Working with an established column of ants, direct sunlight was first shut off by setting up a board beside the trail; then a mirror was placed to reflect sunlight oppositely to the original direction. A typical result in ants such as *Lasius niger* was a clear reversal of traffic, indicating virtual orientation to light direction. Under certain conditions, however, the experiment is not effective with the same species.

Investigating this matter in the laboratory, Brun used Lubbock's procedure of reversing or interchanging cardboard floor sections of an established *Lasius* trail between nest and food-place. He found that when the trail was chemo-polarized (by interchanging floor-sections), a dominant reliance upon the chemical gradient made the ants less dependent upon direction of light than was the case with more homogeneous chemical trails.

In other ant species, such as *Formica*, field experiments demonstrated that, under given conditions, the chemical factor may dominate orientation at given times (*e.g.*, when the path is narrow and canalized), whereas, under other conditions, the visual factor of light direction may dominate (dependent upon compound-eye processes), and, under still other conditions, a visual light-and-shadow factor (dependent upon the ocelli) may dominate. In demonstrating the last point, Brun first established, through observational records of individual foraging trips by *Formica* ants, that a polygonal

* For references on the general subject of orientation in ants, see Brun[6] and Schneirla.[41]

course might be taken, with a succession of definite changes in direction, before the ant headed rather directly for the nest. The use of appropriate tests indicated that chemical and light-direction factors were not responsible. Finally, Brun established a reaction to large objects (*e.g.*, trees) as basic here, through his finding that disorientation occurred when object-masking changed the situation in given ways. Appropriate observation-selective controls also were employed.

Through the combined field and laboratory methods developed in this area,[7] characteristic species differences in the pattern of orientation have been demonstrated, as well as variations in the relative importance of sensory factors under different environmental conditions. As a further step, the maze method may be used in the laboratory, offering a controlled situation essentially equivalent to the situation of foraging in the field, to study the manner in which the way-finding pattern develops through learning.[41,43]

The tendency to be selectively preoccupied with certain results in particular sometimes distracts attention from essentials. For example, Cornetz was led by results of the polygonal-course type described above to minimize visual factors and resort to an "unknown direction sense." The matter was clarified by Brun through further tests and a comparison of results for numerous species under varied environmental conditions. At one stage, it was necessary to demonstrate, contrary to an assertion of Cornetz's, that the foliage of a eucalyptus wood did not exclude directed light and thereby obviate light-compass orientation. A comparable tendency is frequently seen, in the literature on bird migration and homing, to minimize or exclude the role of certain factors (*e.g.*, visual, thermal, food) in favor of some other one in focus at the time. According to a critique by Odum,[32] this error has been made in a recent purported demonstration of magnetic-field orientation in pigeons, in which no adequate controls were introduced on the function of topographical gradients and other environmental aspects favoring visual cues in particular.

An interesting illustration of the way in which direct-manipulative controls advance in field investigation is furnished by some experiments on bird homing. In the well-known experiments of Watson and Lashley[57] with terns, groups of birds were transported over considerable distances, in some cases over hundreds of miles, in different directions from their home on Bird Key in the Tortugas off Florida, and approximately half of them returned successfully. The explanation of their homing over long distances through presumably strange territory is a matter of conjecture, due to the fact that the birds could not be followed. Recently, Griffin and Hock[17] have performed similar experiments with the gannet, transporting the birds to a point more than 100 miles inland from their nesting area on the coast of New Brunswick. A new feature of experimentation was, that upon release, the course of individual birds (in half the cases) was followed by means of an airplane. The plane following above did not affect the behavior of the released bird in its flight, as was indicated by the fact that the frequency of return was the same in the experimental birds and in a control group not followed in the return. There was no indication of a direct flight in the followed birds, through long distances after their release, but all exhibited clear indications of spiralling. The results suggest that some of the birds may have become oriented when they chanced within visual range of landmarks in the coastal area. With this new technique, the orientation process in transport-and-release tests may now be studied effectively with wider controls than before.

Because of the basic reliance of most field investigation upon the observation-selective type of control, for effective analysis and synthesis it is very desirable to survey the results broadly after each test in which a segment is focused upon. The investigator aims at a systematic exploration of the phenomenon. For example, my studies on the army-ant behavior pattern involved, in essence, an examination of the following parts of the system in succession: first, the development and organization of raids; then, the relationship between raiding and emigration; next, the nature of rhythmic processes in colony behavior; and so on.[42] After studying each sub-problem, a renewed concentration upon the pattern as a whole became more advantageous.

At first in this program, with the exception of secondary manipulative controls in studying chemical-trail orientation, only observation-selective procedures were followed. The object was to discover essential events and relationships by significant comparisons through observation. As an outcome of this procedure on a small scale, a major comparison study became possible. A condition was established in which a given colony staged large daily raids and emigrated each night. Through the time, a great brood of developing larvae was present. The hypothesis that a superadded excitatory effect from this brood served to keep the colony maximally active was supported by events when the larval brood came to maturity. Precisely on the day when the brood of grown larvae was enclosed in cocoons and its excitatory effect (presumably) reduced to a minimum, the colony began to stage very small raids, and emigrations ceased. In effect, maturation and enclosure of the brood constituted a control (observationally selected) on the factor of brood stimulation, for no other significant changes were discovered at the time. As a further check, the given colony remained sessile until this brood matured pupally and callow workers emerged, then broke abruptly into its maximal behavior condition of large raids and nightly emigrations. As a direct-manipulative test, the larval brood of a colony (then definitely nomadic) was removed, whereupon the level of raiding decreased sharply and nomadism ceased. Appropriate manipulative tests in the laboratory, and various detailed laboratory observations, confirmed the existence of a strong direct excitatory effect exerted by larvae upon adult workers, in contrast to a relatively weak effect of enclosed pupating broods. The results supported the postulation of a "drive" factor underlying colony behavior changes, exerted at periodic intervals by developing broods. This relationship proved to be the focal process in the highly organized behavior pattern of these social insects.

The essential procedure in such an investigation involves the comparison of major changes in the phenomenon with other conditions, which are focused upon successively, to probe their suspected relationship. As the selective observational studies advance, direct-manipulative tests become possible. Leading alternative hypotheses are checked similarly. For instance, the leading alternative to the above explanation of migration in army ants was the Vosseler concept of food depletion in the nesting area. Among the comparisons which ruled this out, there was the fact that on several occasions, after a given nomadic colony had evacuated its site of the day, another colony settled down in the area for an extended stay. The variations in colony behavior occurred very regularly, but always in relation to identifiable brood changes, and not food supply.

It should be noted that, in field research, we are not merely observing events as concomitant or non-concomitant, as one might pull markers of like or unlike color from a container by chance. Rather, we study concurrent series of events with the object of demonstrating the presence or absence of system inductively, and plan to explore selectively all crucial aspects of the phenomenon and their variations so that the nature of underlying relationships may be revealed. The research is qualitative in the sense that we are examining all relationships indicated as important among the events and processes of a system or pattern. In such instances, the existence and the nature of a pattern cannot be demonstrated readily by quantitative procedures, which are, however, useful when a specialized stage of analysis and synthesis is reached.

The Artifact Method: A Combination of Procedures

An example of a specialized use of direct-manipulative controls in observational investigation is the "artifact method," in which given stimulus-episodes are introduced artificially, to find what aspects of the animal's environment figure critically in its ordinary behavior. Thus, in Audubon's studies of the role of smell in food-location by vultures, objects such as a painting of a sheep's body and a stuffed deer skin were placed on the ground in the open. From the fact that vultures came down to the artifacts but not to covered food, Audubon was drawn to the conclusion that smell could play no great part in the vulture's carrion responses, in contrast to vision.[51] Results were later obtained by Chapman[9] indicating that both turkey buzzards and vultures reacted to hidden carrion on the basis of smell, although a visual guidance to food occurred when it was in the open.

The artifact method has found its most systematic use in the investigations of Tinbergen,[53] with insects, birds, and fishes. A representative study was that of Tinbergen and Kuenen[54] on the appearance of the gaping response in young nestling thrushes. Tactual and visual stimuli of various kinds (*e.g.*, tapping of bill or of nest edge, movement of a stick end or of black discs of different sizes and forms) were presented to the nestlings from an early time. The gaping reaction was first elicited by mechanical stimuli alone. Then visual stimuli began to elicit the response, the most effective artifacts being objects larger than 3 mm. in diameter, such as black discs, moved at or above head level. Shortly after the first visual stimuli produced gaping, it was observed that, when a small convexity protruded from the upper margin of the disc, the gaping of the young bird was distinctively directed toward this part of the stimulus field.

This method is related to the psychophysical "method of limits"[55] in the sense that it involves presenting stimuli in a more or less graded series (*i.e.*, in size, pattern) to find the threshold below which a given activity is not elicited. It is a departure in the sense that aspects of the stimulus (*e.g.*, its size, its figural aspects) are varied, with the object of finding which of them are essential to response under given conditions. The artifact method is similar to the "method of equivalence" as used by Klüver,[25] Lashley,[26] and Maier,[29] in their laboratory studies of mammalian visual discrimination, in that both methods are aimed at finding which of varied types of stimuli effectively produce the same response.*

In such experiments, the investigator's attitude and theory are especially crucial for the selection of stimuli and their manipulative use. One of Tinbergen's[53] remarks about the method is very interesting in this connection: "Experimentation with releasers . . . seems a very simple business indeed. However, this is true only in appearance. The technique is simple enough, but as a method of thinking and planning it has some treacherous pitfalls. It is easy to meddle with animals, to experiment in a vague and random way, but it requires some knowledge of ethology as a whole and some insight into the nature of a given problem to plan really convincing experiments that are relevant to the problem." In other words, the essence of the method is the selection, on the basis of preliminary studies of the animal in its environment, of stimulus patterns or part-patterns judged relevant to the elicitation of a given response, with the object of studying the conditions of appearance of this response and aspects of the pattern essential for its elicitation under given conditions.

The method has been effective for studying behavior such as the early reactions of young birds, and for analysis of stimulus patterns involved in the interaction of members of sexual pairs in different animals. However, the Tinbergen and Kuenen conclusions, for instance, advance beyond such matters to the conclusion that the order of responsiveness to mechanical and to visual stimuli has an entirely innate basis and also that the gaping response proper and the directional character of this response are innately differentiated. It should be considered that the theoretical attitude of the experimenters may have caused them to overlook quite inadvertently the desirability of controls on the influence of experience in these developments. In their study, adequate controls are not apparent on the possibility that extrinsic factors and experience are influential in the sequence of various changes in the gaping of nestlings. For instance, some results obtained by D. Lehrman (unpublished) indicate that there is a critical period during which gaping is first elicited by mechanical stimuli, when the eyes open secondarily during each reaction, thereby introducing incidentally a concomitance of gaping activity and visual effect which may have some importance for the later occurrence of gaping specifically to visual stimulation.

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* The investigation with nestling thrushes was first carried out under laboratory conditions, then was repeated in the field (with adult birds absent in both cases) with entirely comparable results.

To be comprehensive, investigations of this kind, with behavior appearing during early stages of development, must involve distinctive controls on the possible involvement of conditioning or learning factors in the phenomenon.

Cross-Sectional and Longitudinal Investigations Combined

The observation-selection methods may be described as the scheduling of cross-sectional studies of behavior in time so that strategic comparisons may be made within the underlying system. Studies which involve the comparison of a few cross-sectional episodes of behavior must be regarded as tentative and incomplete. When a consecutive series of cross-sectional surveys is made, with investigations timed at intervals during a period in which the pattern is suspected to be undergoing significant developments, a more adequate synthesis can be made. An example of this type of study is the investigation of eel migration carried out by Schmidt,[40] in which the eel population of the North Atlantic ocean was sampled frequently in a spatially systematic way. From the fact that, through one interval of time, young eels increased in size and age as Europe was approached, whereas, through another distinct period, adults in the samples increased in age and sexual maturity westward from Europe, the conclusion was drawn that adult eels migrate westward from Europe to reach a given spawning ground in the ocean, and that young eels (of European species) migrate eastward from this area toward Europe. This kind of investigation approaches the longitudinal type of study, in which behavior trends are followed consecutively through considerable periods of time. For a thoroughgoing coverage of behavior patterns and their effective conditions of origin and change, such a method is imperative, whether we are studying problems in group or individual behavior.

The longitudinal plan, combined with intensive cross-sectional studies, has brought significant results in the investigation of both individual and group phenomena. As concerns individual patterns, a representative example is furnished by study of the pecking response in the chick.[29] The group behavior functions and organization of birds and mammals have been explored advantageously from this point of view, as other authors in this monograph demonstrate. As an example from another level of organization, the writer's experiments on the army ant behavior pattern were designed so that all cross-sectional records of different colonies at critical stages could be compared with (presumably) equivalent stages in given colonies studied over long periods of time. Although shorter studies on different individuals or groups are contributive, beyond doubt the greatest degree of control and depth of comparative study is gained in a programmatic combination of short-term comparisons with long-term surveys. This is particularly true in the study of phenomena which are complexly organized and subject to change in time, as are the cases of individual development and of social organization.*

We should not omit mentioning the fact that in many instances, excellent field research has fallen short of its deserved gains through a concentration upon mature stages of given phenomena to the exclusion of developmental studies. For instance, although the field study of ant way-finding is of long standing and reaches a point of effective theoretical clarity in the work of Rudolf Brun,[6] we are still limited to hypothesis so far as the development of phenomena of field orientation is concerned, or to inferences from laboratory investigation.[41] The paper of Dr. Riess will deal specifically with the important topic of studying developmental phenomena.

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* Of course, there are technical problems to be solved, such as the necessity of marking permanently all individual animals in the study group, if such programs are to be carried out advantageously.

Control in Logical Processes of Investigation

The concept of observation-selective control may be extended into a consideration of the conditions of reliability and validity in any specialized logical processes of investigation. In the behavior literature, controls of this sort may be found not only in the positive but also in the negative sense.

Because perceiving, thinking, and action are related in subtle and complex ways, the mental processes of hypothesis and theory are inevitably involved at all stages of scientific investigation. The desirability of controlling personal factors (such as attitude) in the framing and execution of a project is behind the frequent emphasis upon distinguishing between fact and hypothesis. Such a distinction, although difficult, is desirable, for it should increase our alertness to recognize the marks of our hypothesizing and theorizing, and thereby lead to a more effective use of such processes in reporting the nature of natural phenomena.

From a consideration of psychological processes underlying the observation-selective functions of an observer, even as brief a one as ours has been, it is apparent that the standards of validity in scientific reporting must reach considerably beyond the implications of Karl Pearson's[34] statement that the laws of nature are only descriptions of the order of our perceptions. To point the matter, we may consider Cohen and Nagel's[12] recognition of four different senses in which the word "fact" is frequently used in the literature of science. As illustration, we may consider a hypothetical case in which four statements of "fact" are made by the same observer at four different times. These are, let us say:

1) "The animal was heard to utter two sounds."

2) "The animal uttered a low grunting sound and a high whining sound."

3) "The animal uttered two sounds, a high-pitched 'whining' sound as an expression of hunger, and a low-pitched grunting sound in reaction to a female."

4) "The high-pitched whining sound, a response to hunger, was broken off when the male sighted a female; whereupon the low-pitched grunting sound was made in order to attract her."

All four types of statement will be found in scientific protocols as statements of "fact," in the "*Results*" section of publications as well as in the "*Discussion of Results*" section, although the careful scientist as a rule endeavors to limit his use of the term to statements on a par with the first two. All are "factual" in the sense that all four statements contain evidence bearing on some problem. On the other hand, each contains a degree of interpretive implication and statement of relationship, and it will be noticed that from the first statement to the fourth this aspect increases in prominence and in complexity. As a fifth possibility, a generalization is sometimes offered as a statement of "fact," for example, that

5) "Animals of this species usually leave off their concern with food, and hunger squealing is displaced by grunting, when a female passes, in order to attract the female."

It is clear from these considerations that the term "fact" is frequently used by scientists in very different constructions, which differ in the extent to which "evidence" and "interpretation" are combined in different cases. The "bare datum of evidence" ordinarily regarded as the essence of fact must be recognized as a hypothetical construct; and our problem is to approximate it as validly as we can. But it should be apparent that "fact" in the sense of the hypothetical "bare datum" will not be dealt with validly in behavior reporting as distinct from interpretation, until the role played by initial concepts and "direction"[27] is taken into account.

When initial concepts are strong and vivid, and metaphorically very appealing, they may be carried through an entire study without ever being examined effectively from the standpoint of validity. Stated plainly, this type of study is likely to be deductive rather than mainly inductive, as would appear desirable. The possibility should be recognized that an initial proposition may be sufficiently broad to enfold almost any datum of evidence in the given field in a cloak of indelible deductive coloration. A clear example is the initial statement of Hingston,[21] in his book "Instinct and Intelligence," that "Everybody knows what instinct is." A more subtle one is the assertion of Russell[38] that ". . . inborn impulse to carry out a specific mode of action is the fundamental thing in instinctive behavior. . . ."

The manner in which presumptive concepts may be brought under effective control through a constant checking of earlier processes retroactively is suggested by William James's[23] caution that "The most useful investigator, because the most sensitive observer, is always he whose eager interest in one side of the question is balanced by an equally keen nervousness lest he become deceived."

A good example of an investigator's earnest efforts toward control in gathering and reporting evidence is offered in Jennings's[24] classical studies on protozoan behavior, which have all of the essential aspects of field investigation. The book is an important exercise in the technique of bringing out an inductively established behavior principle, namely the relevance of variability in behavior to the accomplishment of environmental adaptations on the given level. It must be said that, on the whole, Jennings succeeded.[47]

The observer's attitude toward what constitutes an adequate sample of data to represent the phenomenon is dependent to a great extent upon his attitude and initial hypothesis. One extreme is represented by the "anecdotal tendency,"[56] popularized by the Plinys and still in evidence in the public prints. Typically, a single outstanding case, considered representative and strikingly convincing in itself, is recounted to "prove the point." The storyteller is not out to *test* the adequacy of his view. Rather, he undertakes to convince the skeptics that his interpretation is the only one. Quite often, validity and reliability are implied by virtue of good social reputation or a "long experience close to nature."* Often, the account is very eloquently and sincerely presented, as in an article in which a "veteran guide"[39] recounts several instances in which animal sagacity is proved, as, for instance, a case in which a "smart little wolf" used a bull elk to dig out mice for him, and another in which beavers rebuilt a destroyed dam by ingenious devices involving reasoning. In each instance, there is a single observation, reported sincerely but with a heavy load of assumption and emotionally toned words. In his answer to the article from the standpoint of the scientific student of animal behavior, Beach[4] emphasized in particular the incompleteness of such reports, as well as the tendency to overlook alternative interpretations involving fewer assumptions. Scientific field investigators will sympathize with the attitude of the anecdotalist who is fond of animals and is struck by their apparent brilliance on occasion. Yet they also know that a single observation, especially when incomplete and reported from "observational memory," can have no valid bearing on the solution of a problem.

The question of validity in field notes obviously involves the fact that our language is loaded with pre-experimental terms, which govern the use of specific imagery in our metaphors, and often dictate thought patterns which canalize our perception and our thinking. Validity is promoted in field records when metaphorical terms and "as if" devices are put in quotes, a practice which encourages later re-examination of the account for soundness of expression. It often happens that conceptual terms, first used as convenient symbols for partially understood things and relationships, slip through automatic transitions into a permanent form. No important term should be kept in use without frequent careful examination, for the unchallenged crystallization of a key concept in a much used verbal expression may prevent the observer from ever noticing exceptions to its chief implications.

An adequate observation-selective procedure calls for a carefully planned and consecutive study. As an example, let us take a hypothetical investigation of "fighting" between males of a given species of mammal, in its possible relation to mating. Evidence is needed which will permit testing available hypotheses logically. To broaden our receptivity, we focus, to begin with, on how fighting comes about, then on possible relations of fighting to other activities in the species. First, we must obtain as adequate an account of all cases of combat and their conditions as possible, both in and out of rutting season. We collect data on the relative frequency of variations in the initiation and conduct of combat. To test the hypothesis of a direct sexual-selective function of fighting, we would take note of the conduct of participants and other members of the group after each fight. If the "loser" then mates as frequently as the "winner," perhaps fighting does not play a direct part in sexual selection but has some other role, such as facilitating reproduction in a generalized manner. This hypothesis would then be examined appropriately, and so on.

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* Long experience close to nature may make an anecdotalist into an artist in that practice, or may make him a valid reporter of events, depending, for one thing, upon his developing an interest in scientific validity.

In our study of the representative phenomenon and its variations, reliability and validity are promoted by repeating studies, to check on what is relevant to the phenomenon, the order of importance of relevant aspects, and other points. Once the principal pattern of factors and relationships is outlined, in further studies our leading hypothesis may be checked back into the phenomenon under selected variations in conditions. Such a review of occurrences, with a new approach to the phenomenon, may afford a needed control by reducing the canalizing effect of a previously dominant attitude which emphasizes certain items and excludes others.

The need to re-examine our initial premises at intervals, in the light of current findings, may be illustrated in terms of a frequent cause of ambiguity, a confusion of the factual existence of adaptive behavior systems with the hypothesis of purposive causation. The fact of adaptivity concerns the extent to which given activities adjust the animal to, or fit it for, its life zone. This aspect of behavior has no necessary relation to complex psychological functions such as anticipation and purpose, although McDougall[30] and some others have treated them as virtually synonymous. The property of adaptive function is common in the behavior patterns of animals from amoeba to man, but without the demonstrated involvement of anticipation or purpose except in the higher vertebrates.[29] The danger of generalized expressions for adaptive adjustments in behavior, such as Russell's use of "perception" and "objective purpose" on all levels, is that they obscure important differences which appear to exist in the nature of psychological processes underlying adaptive adjustment at different phyletic levels.

The fact-gathering and interpretive aspects of science are closely related. We start out in laboratory and in field, in observation and experiment alike, by noting resemblances. But *degrees* of similarity are often important and sometimes crucial, and, by watching out for them and using special techniques to identify them, as by quantifying the main aspects of behavior, we may uncover important relationships of difference in our phenomena. Our in vestigation thereby constitutes an analysis of the phenomenon, which centers around the comparison of events and relationships in situations (*e.g.*, social groups) which are similar in some respect considered important. When a number of different types of phenomena are assigned to a common category (*e.g.*, Alverdes's[2] "open society"), the grouping must be considered tentative in dependence upon the extent to which the essential basis of similarity has been demonstrated. The process of synthesis, in which a theory is constructed to interpret the nature of a given behavior pattern or the interrelationship of a series of such patterns, often hinges upon the extent to which biological processes underlying the various behavioral events have been examined.

The Comparative Method in Field and Laboratory Investigation

The advantages of the comparative method to the processes of analysis and synthesis in animal study are clear. A difference in the homologous behavior patterns of two closely related species frequently is critically useful in uncovering important problems or basic principles. For example, by a comparison of group functions in the red deer and the roe deer of Scotland, Darling[13] found a significant difference meriting further examination, that, in the matriarchal groups of red deer, a close social organization prevailed, whereas organization was considerably looser in the roe groups with buck leadership. The advantages of species comparisons are demonstrated in this monograph, for example, in the papers of J. P. Scott on social behavior of dogs and wolves and of J. W. Scott on species of grouse.

As an example from another level, it was helpful in studying the basis of migration in army ants to note, first of all, that daily emigrations occurred in two closely related species despite wide differences in their patterns of raiding.[42, 44, 48] A comparison of the relationship between raiding and the daily emigration process in colonies of the two species clarified the part played by similar factors, such as the process of afternoon rearousal of raiding in particular. Thereby the essentials of nomadic behavior in the general group became more apparent.

The ideal program for the future study of animal behavior would involve a coordination of field and laboratory investigation. Each has its characteristic advantages. Field investigation offers an opportunity to work with the animal's full pattern of activities from various approaches, with a broad perspective, with the relevance and, to a great extent, the validity of laboratory findings in view. In the laboratory, one may focus on specialized problems such as sensory discrimination, motivation, learning, and higher processes, pursuing them in detail and under conditions involving refined controls. Such studies require a further unification which may be gained in field applications and extensions. Programmatic studies along these lines may be anticipated.

If we know the typical behavior pattern of a given animal under natural conditions, and its usual variations, as well as the range of natural conditions to which the animal is capable of adjusting, the manner in which it may be investigated to advantage in the laboratory becomes clarified. Then the nature of crucial aspects of natural adjustment may be explored, as in gradient tests, discrimination and sensitivity tests, tests of adjustment through learning, and others as appropriate. Such a coordination of efforts will ward off errors in the planning of laboratory problem environments. Such difficulties have been apparent in the past, in that too little attention has been paid to the influence of the laboratory environment, the cage, on the functioning of laboratory animals in problem situations. It is only recently that serious study has been turned to such matters for animals in laboratory[36] and zoo environments.[19] Hediger's comparison of the effects of confinement on caged animals, in relation to their behavior patterns in the wild, is certainly of interest from the standpoint of work with cage-confined laboratory animals also.

To represent one aspect of this important type of problem which has been much neglected, we may consider the fact that, in the case of confined animals, there is certain to be a considerable variation in activity, according to organic condition and related factors. Despite the fact that degrees of difference in the tendency to vary activity appear to be important for animal responsiveness under differing organic conditions, our chief tests have involved offering an opportunity for *homogeneous* activity, as in the exercise wheel. Measures such as Dashiell's[14] "exploratory maze" and Whitaker's[58] light-dark cage represent a partial escape from the idea that measuring "general activity" brings responsiveness adequately under measurement. These matters call for a reappraisal of methods and procedures from the standpoint of field-laboratory environmental conditions and their effects upon animal personality, considered comparatively.

We may agree in part with the European criticism[52] that in some respects American investigators have become overspecialized on certain laboratory problems and that a preoccupation has developed to some extent with specialized methods for their own sakes. In part, such tendencies may be due to ethnocentric attitudes which have influenced the planning of laboratory projects.[46] It is to be expected that the artificialities often seen on this basis will be reduced in laboratory study which is planned more adequately in relation to the animal's situation under natural conditions.

It is probable that projects calling for the correlated investigation of given problems in laboratory and field will be undertaken more frequently and extensively when more field stations are available at which behavior studies may be carried out to advantage in typical ecological settings. Situations are desirable where a certain amount of laboratory investigation can be done in connection with a field program, to test possibilities for more extensively controlled work in regular laboratories. From the laboratory side, in addition to devising new experimental methods which will fit the special conditions and needs of the field, some of our most transportable and conformable methods may be used in the field. It is evident, for example, that more should be known of how far an animal's adaptations in the natural situation of the species are influenced by its capacities for learning and plastic behavior in general. Environmental emergencies of appropriate types may be devised to study how various obstructions are met, and comparable methods may be developed for investigating the establishment of behavior routines under natural conditions. For example, Gordon[16] used a variety of standard laboratory tests, including jumping situation to test discrimination, simple mazes, problem boxes, and string problems, to test the capacities of the western chipmunk in its native habitat. It should be possible to carry many of our laboratory methods into a direct-manipulative use in the field, with appropriate modifications. The possibilities are promising, and open the way for the comparative use of a great body of laboratory evidence.

An important question awaiting investigation concerns the extent to which animals under natural conditions are led to use their potentialities for plastic adjustments through learning and higher processes. Nissen[31] was led to the conclusion that the chimpanzees he observed in French Guinea were not very much extended to employ such capacities in this habitat: "It is hardly surprising that when wants can be satisfied by what we may call primitive behavior, complicated and therefore difficult behavior mechanisms will not be brought into play, even if potentially present." He thought the emotional aspects of life in these chimpanzees were much more developed, relatively, than the intelligence capacities, as compared with known laboratory conditions of behavior. What differences may be found on this point within the same species under differing environmental conditions, and from species to species under the respectively characteristic environmental conditions, remain to be investigated.

Not only do field and laboratory supplement each other in these respects, they also may be used to correct each other in appraising the relative prominence of different capacities in the two general settings. Carpenter[8] concluded that laboratory investigations of an animal such as the gibbon help to disclose possible misjudgments in the relative prominence of characteristics in the field, such as the minimizing of how far sensory capacities are used and the emphasizing of motor capacities. At the same time, he notes that there are problems, such as group organization, intergroup relations, and communicative behavior, which may be first and most validly studied in free-ranging animals under natural conditions. Further control will be obtained in planning investigations and in the interpretation of results when laboratory findings are referred to the field and field results to the laboratory as a matter of course.

Resumé

To sum up, our purpose has been to show that, in each type of problem in animal psychology, there exist opportunities for correlated field and laboratory research. These problems may be pursued most adequately in the field when we think of field and laboratory research as basically similar. We have considered several means whereby control, in the sense of greater adequacy, may be obtained through emphasis upon training, upon the technique of the observer's approach to the problem and situation, through his strategy in selecting variations for study in contrast, and through adequate techniques in logical operations.

Working with animal behavior under natural conditions, the problems of reliability and validity in the collection and interpretation of data begin with the observer's perception. The influence of his attitudes and pattern of thinking begins with his selection of a problem and his preliminary survey of the field. By recognizing the essential function of hypothesis and other logical processes, such as analysis, synthesis, and comparison, from early to late stages in the gathering and interpretive use of evidence, methods may be worked out to bring their influences under control and improve their dependability.

Observation-selective controls involve the basic techniques of field method, from the perceiving of a phenomenon, and its regulated variation, to measures promoting exactness in taking records and rechecking them at suitable intervals. The concept of control subsumes our attitude toward the problem and its characteristics, which governs whether important relationships involved and factors underlying the phenomenon will be explored in adequate ways. From these considerations, programs become most comprehensive when investigation of the phenomenon is varied systematically in both a cross-sectional and a longitudinal sense. As an investigation proceeds, ways in which the direct-manipulative type of control may be applied will become apparent, according to the nature of the phenomenon studied. The study of natural phenomena from the standpoint of their developmental stages is a necessary feature of method in field investigation.

Errors attributable to the psychology of the investigator will not be eliminated through using supplementary instrumental methods, because these will be used according to his observation-selective techniques. The nature of these techniques will dominate his procedures in quantifying the records, in selecting instruments and determining their use in time and space, and in selecting and introducing direct-manipulative procedures of any character. These and other modes of extending the scope of field observation are subject to systematic controls similar to those needed for "bare observation." Supplementary methods are especially valuable when they sharpen attention to the basic phenomenon and promote a thoroughgoing exploration of its aspects through systematic variations.

Thus, control is gained in the field, not simply by mechanizing or quantifying our work or by multiplying cases, but by repeating given aspects of the investigation under methodically varied conditions. The object is to derive an adequate interpretation of the phenomenon through the logical processes of comparison, analysis, and synthesis. In the sense of psychological control (over attention, perception, and reasoning in the problem situation), the object is gained by means of systematically shifting our direction of approach to the problem, as concerns aspects of environment and animal, and relationships disclosed as important. Such procedures, if applied adequately to research from the preliminary stage of general observation to the specialized stages, should lead to planning more intensive investigation along new or expanded lines. In these respects, a close coordination of field and laboratory work is to be encouraged. The experimental attitude should play a leading role at all stages in field investigation.

Bibliography

1. Allee, W. C. 1945. Social biology of subhuman groups. Sociometry **8:** 21–29.
2. Alverdes, F. 1927. Social Life in the Animal World. Harcourt, Brace. New York.
3. Bartlett, F. C. 1932. Remembering: A Study in Experimental and Social Psychology. University Press. Cambridge.
4. Beach, F. A. 1947. Of course animals can think. Nat. Hist. **51:** 116–118, 144.
5. Boring, E. G. 1929. A History of Experimental Psychology. Appleton-Century. New York.
6. Brun, R. 1914. Das Raumorientierung der Ameisen und das Orientierungsproblem im Allgemeinen. Gustav Fischer. Jena.
7. Brun, R. 1926. Psychologische Forschungen an Ameisen. Abderhalden's Handbuch der biologischen Arbeitsmethoden. Abt. VI, Teil D, Methoden der Vergleichenden Tierpsychologie. Pp. 179–230.
8. Carpenter, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon (Hylobates Lar). Comp. Psych. Monogr. **16**(5): 212.
9. Chapman, F. 1938. Life in an Air Castle. Appleton-Century. New York.
10. Churchman, C. W. 1948. Theory of Experimental Inference. Macmillan Co. New York.
11. Cohen, M. R. 1931. Reason and Nature. Harcourt, Brace. New York.

12. Cohen, M. & E. Nagel. 1934. An Introduction to Logic and Scientific Method. Harcourt, Brace. New York.
13. Darling, F. F. 1937. A Herd of Red Deer. Oxford. London.
14. Dashiell, J. F. 1925. A quantitative demonstration of animal drive. Jour. Comp. Psych. **5:** 205–209.
15. Fisher, R. A. 1935. The Design of Experiments. Oliver and Boyd. London.
16. Gordon, K. 1943. The natural history and behavior of the western chipmunk and the mantled ground squirrel. Oregon St. Mon., Zool., No. 5: pp. 104.
17. Griffin, Donald R. and Raymond J. Hock. 1948. Experiments on bird navigation. Science **107** (2779): 347–349.
18. Haring, D. G. and Mary E. Johnson. 1940. Order and Possibility in Social Life. Smith. New York.
19. Hediger, H. 1942. Wildtiere in Gefangenschaft. Benno Schwabe & Co. Basel.
20. Heidbreder, Edna. 1924. An experimental study of thinking. Arch. Psychol. No. 73.
21. Hingston, R. W. G. 1928. Problems of Instinct and Intelligence. Macmillan. New York.
22. Hudson, W. H. 1893. Idle Days in Patagonia. Appleton. New York.
23. James, W. 1896. Will to Believe, and Other Essays in Popular Philosophy. Longmans, Green. New York.
24. Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia. New York.
25. Klüver, H. 1933. Behavior Mechanisms in Monkeys. Univ. Chicago Press. Chicago.
26. Lashley, K. S. 1938. The mechanism of vision: XV. Preliminary studies of the rat's capacity for detail vision. Jour. Gen. Psychol. **18:** 123–193.
27. Maier, N. R. F. 1930. Reasoning in humans. I. On direction. Jour. Comp. Psych. **10:** 115–144.
28. Maier, N. R. F. 1939. Qualitative differences in the learning of rats in a discrimination situation. Jour. Comp. Psych. **27:** 289–327.
29. Maier, N. R. F. & T. C. Schneirla. 1935. Principles of Animal Psychology. McGraw-Hill. New York.
30. McDougall, W. T. 1924. Outline of Psychology. Charles Scribner's Sons. New York.
31. Nissen, H. W. 1931. A field study of the chimpanzee. Comp. Psych. Monogr. **8** (36): 122.
32. Odum, H. T. 1948. The bird navigation controversy. Auk **65:** 584–597.
33. Pearl, R. 1911. The personal equation in breeding experiments involving certain characters of maize. Biol. Bull. **21:** 339–366.
34. Pearson, K. 1900. The Grammar of Science. Black. London.
35. Poincairé, H. 1912. La Valeur de la Science. Flammarion. Paris.
36. Riess, B. F. 1945. "Freezing" behavior in rats and its social causation. Jour. Soc. Psychol. **24:** 249–257.
37. Rosenthal-Schneider, Ilse. 1945. The scientist's interference with the things he studies. Australian Jour. Sci. **7:** 166–169.
38. Russell, E. S. 1944. The stereotypy of instinctive behavior (with an appendix on valence as "meaning for action"). Proc. Linn. Soc. London, 155th Session, Pt. **2:** 186–208.
39. Russell, G. A. 1946. Can animals think? Nat. Hist. **55:** 478–480; 490–492.
40. Schmidt, E. J. 1922. The breeding places of the eel. Phil. Trans. Roy. Soc. London, Series B, **211:** 179–208.
41. Schneirla, T. C. 1929. Learning and orientation in ants. Comp. Psychol. Monogr. **6:** 1–143.
42. Schneirla, T. C. 1938. A theory of army-ant behavior based upon the analysis of activities in a representative species. Jour. Comp. Psychol. **25:** 51–90.
43. Schneirla, T. C. 1942. The nature of ant learning. II. Jour. Comp. Psychol. **35:** 149–176.
44. Schneirla, T. C. 1945. The army-ant behavior pattern: nomad-statary relations in the swarmers and the problem of migration. Biol. Bull. **88:** 166–193.
45. Schneirla, T. C. 1946a. Problems in the biopsychology of social organization. Jour. Abnormal & Soc. Psychol. **41:** 385–402.
46. Schneirla, T. C. 1946b. Contemporary American animal psychology in perspective. Twentieth Century Psychology, 306–316. Philosophical Library. New York.
47. Schneirla, T. C. 1947. Herbert Spencer Jennings: 1868–1947. Amer. Jour Psychol. **60:** 447–450.

48. Schneirla, T. C. 1949. Army-ant life and behavior under dry-season conditions. III. The course of reproduction and colony behavior. Bull. Amer. Mus. Nat. Hist. 95.

49. Shelford, V. E. 1929. Laboratory and Field Ecology. Williams & Wilkins. Baltimore.

50. Sherif, M. & H. Cantril. 1945. The psychology of "attitudes." Psychol. Rev. **52:** 295–319; **53:** 1–24.

51. Strong, R. M. 1911. On the olfactory organs and the sense of smell in birds. Jour. Morph. **22:** 619–662.

52. Tinbergen, N. 1942. An objectivistic study of the innate behaviour of animals. Bibliotheca Biotheoretica, Ser. D, **1** (2): 39–98.

53. Tinbergen, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull. **60** (1): 6–51.

54. Tinbergen, N. & D. J. Kuenen. 1939. Über die auslösenden und die richtunggebenden Reizsituationen der Sperrbewegung von jungen Drosseln. (Turdus merula L. und T. e. ericetorum Turton). Zeitschr. Tierpsychol. **3:** 37–60.

55. Titchener, E. B. 1915. Experimental Psychology. Vol. II. Quantitative Experiments. Part II. Instructor's Manual. Macmillan. New York.

56. Warden, C. J., T. N. Jenkins, & L. H. Warner. 1940. Comparative Psychology; A Comprehensive Treatise. Vol. I. Principles and Methods. Ronald Press. New York.

57. Watson, J. B. & K. S. Lashley. 1915. Homing and related activities of birds. Carn. Inst. Wash., Publ. No. 211: 9–60.

58. Whitaker, W. L. 1937. A method for studying environmental choices of laboratory animals. Science **86:** 314.

59. Wolf, A. 1929. Scientific method. Encyclopedia Brit., 14th Edition **20:** 127–133.

60. Woodworth, R. S. 1937. Situation-and-goal set. Amer. Jour. Psychol. **50:** 130–140.

MEASUREMENT OF SOME PHYSIOLOGICAL REACTIONS TO ARCTIC CONDITIONS

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Wars arise when people conflict at geographical frontiers, and out of these impacts a confusion of opinion develops which impels people, in ignorance, to resort to arms and prevents them from gaining, through knowledge, the advantages of working and thinking for the common interest of the world. Science is now universally recognized as a significant factor in the welfare of nations, and it became important to determine how physiology could most help to throw the light of reason upon world affairs. It seemed certain that a great contribution could be made in the determination of the physiological reactions to difficult conditions, whether these be geographical, climatic, or social or those arising through the new orders of power and speed which are at hand. It appeared likely that one group of physiologists would deal with both geographic and climatic stresses affecting life, and, after conferences and discussions, in which the National Research Council and the Research and Development Board gave their interested and critical attention, it was decided to go ahead on a program of research called "expeditionary physiology."

Simultaneously, a strong interest in biological research under natural conditions was developing among another group of biologists, who were primarily concerned with behavioral aspects of animal societies, and it was agreed, in organizing means for these two different methods of research in the field, that the near identity of motives confirmed their value and the correctness of the approach. Since then, the writer has watched with interest the development of the Committee for the Study of Animal Societies under Natural Conditions, the progress of its members' field studies, and the establishment of its remarkable institution at Jackson Hole.

The Arctic Research Laboratory. The purpose of this paper is to account briefly for the progress which has been made in expeditionary physiology. My concern with broader aspects of organization has recently been latent because of my connection with a research project in expeditionary physiology, under the sponsorship of the Office of Naval Research, which has led me, with a group of about fifteen scientists, into concurrent field studies in problems of tropical, desert, and Arctic physiology. The emphasis has been strongest upon Arctic problems, because the Navy is conducting an intensive exploration for petroleum on the Arctic Slope of Alaska, which is that great area north of the Brooks Range, extending to the Arctic Sea.

The field center of this activity is Point Barrow, Alaska, and the broad outlook of the Navy, expressed through the Director of Petroleum Reserves, Commodore W. R. Greenman, has associated with the exploration for petroleum the assistance of a number of important scientific and technical activities. Some of these are the U. S. Geological Survey, U. S. Coast and Geodetic Survey, Arctic Test Station, Civil Aeronautics Authority, U.

S. Weather Bureau, Bureau of Standards, and Office of Naval Research. In this association, the various groups provide funds necessary for their own activities, but their operation is made possible through the knowledge and interest of the entire organization for petroleum exploration.

After obtaining favorable opinions on the establishment of an Arctic Research Laboratory, the Office of Naval Research has proceeded to erect it. Dr. M. C. Shelesnyak of the Office of Naval Research first outlined the need for such an institution, and his demonstration of the importance of this projected laboratory has led to the considerable progress which has been made in its establishment.

The first group of about ten scientists from Swarthmore and Cornell arrived at Point Barrow in August, 1947, to investigate the physiological reactions of animals to Arctic conditions. The first laboratory was housed in a 20 × 40 Quonset hut, which was adequate for the needs of the first winter. Since the general program for basic scientific research in the Arctic called for physical, as well as natural, sciences and descriptive, experimental, and theoretical research, increase of personnel to 31 was planned in the summer of 1948, and a 40 × 100 foot Quonset building was erected and equipped as a modern laboratory for basic research on the Arctic Coast of Alaska. The laboratory is well adapted for research. It is not a makeshift affair, and it affords conditions equal to many in the States and facilities for research which are generally superior.

The important facilities connected with the Arctic Research Laboratory are provided through an arrangement between the Office of Naval Research and the Director of the Naval Petroleum Reserves whereby the operating contractors, formerly under the direction of the Naval engineer officer in charge, Commander P. W. Roberts, and now under Commander G. E. Fischer, provide messing facilities, construction, shop services, supplies, and ground and air transportation. All of these services operate with great competence at the rapid tempo of the exploration for petroleum. Work goes on during nine-hour days for seven-day weeks with no letup for holidays.

As a result, the progress of research is surprising and gratifying. In spite of high labor and transportation costs, the uncommon skill and diligence of labor and competence of direction have erected the laboratory at a cost not only below our estimates but, I believe, at lower cost and in much shorter time than required for similar construction in the States. This accomplishment is viewed with great satisfaction, for it represents an example of most effective cooperation among several organizations of a government service in support of a project directed and operated by civilian scientists. The writer, who has had considerable experience with the government, having served in the Army and Air Force and presently being designated Scientific Director of the Arctic Research Laboratory by the Chief of Naval Research, believes that the Laboratory represents a new and sound example of a good kind of relation between civilian scientists and the Navy, which we as scientists should appreciate and will work to maintain.

The Arctic Research Laboratory has been described in this discussion of methods because it is an example of a combination of men and many facilities brought together for the scientific exploration of the Arctic frontier. It is well located for that purpose, being at the most northerly projection of Alaska into the Arctic Sea, where conditions reduce the resident mammals to a few species and restrict the activity of plants and cold-blooded land animals to a few months in the year. However, life is neither sparse nor uninteresting. The dredging operations of Professor MacGinitie in the first summer brought up some 300 marine invertebrate species, representing all phyla and showing many new taxonomic associations. Of land mammals, there are only a few common species—one or two mice and shrews, two lemmings, a ground squirrel (*Citellus*), small and large weasels, Arctic and colored foxes, wolves, caribou, and brown bears. A few moose are spread through the willow and alder bushes of the valleys almost to the Arctic coast.

On the sea ice, there are Polar bears, Arctic fox, and bearded and hair seals—all supported by marine fish and invertebrates. Although the weather appears inhospitable to mammals, with over two months of winter darkness, lakes and rivers frozen for about ten months, and ground which never thaws below a depth of eighteen inches, the animals flourish because they make good use of their abilities and opportunities.

The dominant influence of cold determines which animals can exist, and those which are present show ability to live in ways which give us a new perspective on the means utilized by animals for the preservation of their body temperature. It was assumed that Arctic animals would show adaptations to meet cold, but we did not anticipate the impressive way in which their physiology responds to Arctic conditions nor the clarity with which they have demonstrated to us new physiological methods of investigation.

Field research in physiology has a greater chance for success in an area where extreme conditions have molded animals' behavior to fit a pattern rigidly imposed by the environment, and, through a most fortunate association, we obtain in a favorable Arctic location the logistic support which makes scientific exploration practical. Mention should also be made of the great assistance which we receive from the Eskimos. They are skillful hunters, reliable observers, able mechanics, and interesting and most agreeable associates. With their help, we can go anywhere in the Arctic with our eyes open.

We are also fortunate in that, for ten years, Dr. P. F. Scholander, with a number of associates, has been preparing methods suitable for accurate physiological experimentation in the field. Through his perception of good experimental objectives and with the experience of a good armament of methods tested on numerous civil and military expeditions, we now have obtained a number of instruments necessary for research on the odd sizes and various characteristics of animals which occur in many diverse natural conditions.

Experiments on Metabolism under Arctic Conditions. To illustrate better the objectives in view in expeditionary physiology, I wish to outline briefly some experiments which Dr. Harald Erikson has carried out at Point Barrow. The ground squirrels, *Citellus* sp., of the Arctic Slope force themselves upon the attention by their abundance. These "sic sic" of the Eskimos, weighing about a thousand grams, can be seen in summer on every sandy elevation (and old wind-formed dunes are widespread) and on well-drained hillsides. They are probably one of the largest Arctic converters of plant food into flesh.

It is impressive that they have a very short productive season, for they do not commonly emerge in snow or wet weather, so that their feeding season does not exceed three months; yet digging through their burrows I have not found significant stores of food. We have set about finding out how these small, short-haired animals prepare within themselves for a nine-month fast in frozen Arctic ground.

They adjust well to captivity, except that they are pugnacious and unable to endure wet; but they are undisturbed and undaunted by repeated handling. During three weeks in August, six of our squirrels increased in weight by about 10 per cent.

The first experiments were aimed at showing the relation between oxygen consumption and the surrounding temperature. For this purpose, the squirrel was placed in a closed box, through which air was drawn and collected in a measuring spirometer. From this, samples were withdrawn for analysis. Activity of the squirrels was observed to be related to temperature, for above 21° quiet was maintained during all but 2 out of 55 observation periods. With lower temperature, activity increased until it prevailed between $-10°$ and $-19°$ in all 5 observation periods. The activity increased metabolism, so that at the lowest temperatures the maximum rate was several times that of the quiet periods at slightly warmer temperatures. The quiet rate scarcely increased, however, beyond the experimental range of variation between $+50°$ and $-10°$. Maintained near uniform quiet, metabolism over this wide range of temperature is not observed among animals from temperate climates, and, in the Arctic squirrels, there is indicated a conservatism in the expenditure of energy under the stress of temperature which has also been remarked in several other Arctic birds and mammals.

An examination of the CO_2 production in these experiments made it apparent that its ratio to oxygen consumed, or respiratory quotient, became less at lower temperatures. Below 0° the ratios were between 0.8 and 0.9, above 0° the ratios were above 1.0, and above 20° the ratios lay between 1.1 and 1.2.

There are two observations to make from the survey of the respiratory quotients. At higher temperatures, the animals convert carbohydrate of their food into fat, a storage procedure which is also evidenced by the gain in weight. At R.Q. 1.2, which was common at 20°, a certain portion of metabolic energy is applied to the synthesis of fat. As part of the energy used for the synthesis of fat does not appear as heat, but is stored for later use, it is apparent that the metabolism at high temperatures is more conservative than appears from the oxygen consumption. How the control of fat synthesis is regulated in relation to temperature cannot now be suggested, but the value of that regulation to the metabolic economy of the animal is obvious.

The ability of the squirrels to tolerate temperatures above 40° is more striking than their endurance of cold, because these are Arctic animals. Arctic weasels, snow buntings, foxes, dogs, and Polar bear cubs endure heat well, however, whereas the Schmidt-Nielsens have observed that desert-dwelling kangaroo rats are unable to endure temperatures above 30°. Other observations show that some temperate or tropical mammals are not so resistant to the effects of heat as Arctic animals. It is now cautiously suggested that the Arctic animals, under stress of extreme cold, not only develop good means of insulation against cold by their barriers of fur and feathers, but, in their precision control of metabolism and accurate regulation of peripheral circulation, they develop a physiological mechanism which is effective against heat as well as against cold. These subjects will soon be examined in experiments which are under preparation in the tropics.

Mr. Emminger Stewart observed the body temperature of the squirrels by means of rectal measurements with thermocouples. Between −30° and +30° the body temperature was maintained within a degree of 38° for many hours. In air at 35° the body temperature rose about a degree, which could be sustained for at least several hours. Above 40° the body temperature rose steadily, and these higher temperatures could not be lastingly endured.

During the summer observations, no evidence was observed that the squirrels evade their functions as warm-blooded animals by subsiding into hibernation even after exposure to −30° for 24 hours. During the summer, the squirrels appear to use active measures to conserve their supplies of energy, while remaining consistently alert as warm-blooded animals, ready to seek any means for gathering the food necessary in the brief period of productive physiological enterprise which is open to them.

The observations upon these small Arctic animals raise a number of new physiological problems, which are the more significant because the genus *Citellus* extends, with comparatively slight differences in general habits, far south into the hot climates of the American desert regions. The problems which are raised in the Arctic will not be solved until studied in their counterparts in the tropical temperatures. It is believed, however, that, out of the emphasis of views obtained in the extreme conditions, will emerge much better views of the physiological reactions in mean or temperate conditions.

I appreciate this opportunity to present to you the wide range of facilities and methods of physiological research now made available through the Arctic Research Laboratory. To my mind the most profitable advances in biology can be made through the selection of the natural environments suitable for the examination of the severest biological stresses of geography and climate. In making use of these situations in the field, we will be developing biology as a science; we will also be substituting a confident knowledge of how to live in difficult environments for the widespread apprehension now prevailing at those frontiers, where men and nations, in ignorant conflict with the stresses of climate and geography, are most likely to turn upon each other.

Summary. Ground squirrels of the genus *Citellus*, called "sic-sic" by the Eskimos, live in numerous colonies in favorable locations from the Brooks Range to the Arctic Coast of Alaska. During three summer months, they

are active. In the remaining months, food is apparently unobtainable and, as we have not found sufficient food stores in their burrows or signs of their emergence, it is assumed that they survive in hibernation for about eight months without food and in frozen ground.

Because of their abundance, the "sic-sic" are very important to the metabolic system of Arctic animals. Their survival in conditions apparently so severe from the view point of temperate regions has prompted us to investigate their metabolic economy. The experiments have been carried out by Dr. Harald Erikson at the Arctic Research Laboratory at Point Barrow, Alaska.

During the summer experiments of Dr. Erikson, the squirrels have withstood temperatures of $-30°$ for six hours and up to $+50°$ for a brief period. Measurements of their respiratory exchange have shown that the oxygen consumption increases at the lower temperatures, but the CO_2 output increases to a smaller extent. From several criteria, the resulting respiratory quotient indicates that the metabolic formation of fat from a diet principally of carbohydrate proceeds actively at temperatures above freezing. This is a logical expectation in animals which must prepare, in the brief summer, reserves for such a long winter.

The tolerance of these animals for heat is remarkable, but it has been observed that other mammals of the Arctic Coast—weasels, foxes, dogs, and polar bear cubs—tolerate rather high as well as low temperatures. In fact, this tolerance of heat exceeds that observed by Dr. Knut Schmidt-Nielsen in pack and kangaroo rats from the southern Arizona desert.

INSTRUCTIONS FOR THE MEASUREMENT OF PHYSIOLOGICAL REACTIONS OF UNRESTRAINED ANIMALS

By J. L. Fuller

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The members of an animal society are not interchangeable units, but show individuality in many aspects of behavior. This is frequently the case with behavior which is characterized in common speech as emotional. Over a period of fifty or more years, physiologists have studied numerous visceral responses which result from stimulation and have made progress in elucidating the central nervous mechanisms producing these reactions. In dealing with animals, such functions as heart rate, respiration rate, blood pressure, and blood sugar level may be considered as objective, but somewhat hidden, measures of emotional level.[3]

Psychologists, while accepting the work of physiologists, have a different sphere of interest. Emotions may be regarded as allied to feelings and attitudes—thus, as sets which influence social behavior. In their fully developed form, emotions have been characterized as disorganizing, as when a "fear-paralyzed" animal cannot escape from a predator. Some authors[4] have attempted to deal with behavior without bringing in the concept of "emotion," and it is true that no sharp line can be drawn between emotional and nonemotional behavior patterns. When an animal's behavior is strongly goal directed and many effector systems are involved (either greatly activated or inhibited), it is said to be at a high emotional level.

If one were to attempt to integrate the contributions of investigators from the various disciplines, the following scheme might be acceptable. The overt and covert signs of emotional reaction are not conspicuous at birth. Scott's[8] study of the dog indicates that timidity and playful aggression are apparent at the end of 4 weeks, while tail wagging and similar friendly responses are visible at 5 weeks. The fundamental patterns are unlearned but are modified by age, presumably by the combined effects of maturation and experience. Emotional responses can be conditioned, as can more simple reflexes, and the various emotional patterns may then be aroused by a variety of stimulus situations.

The conditioning mechanism seems to be located in the cerebral cortex. Bard[2] has demonstrated that the rage pattern in cats is released by destruction of a relatively small cortical area—the amygdala and pyriform lobes. The operated animals are easily stimulated to rage. In terms of the hypothalamic theory of Bard and Cannon, release of cortical inhibition produces the emotional response. It is not improbable[1] that excitatory cortico-thalamic effects are also involved, and that these are responsible for the variations in patterns seen in the different emotions, and in different individuals.

That the visceral patterns of response do show individual variation in the laboratory has been shown by Liddell in sheep and goats and by the writer[5] in dogs. Some of our dogs subjected to threats or loud sounds showed marked deceleration of the heart, resembling the effects of direct vagus stimulation. The more usual response, however, is an increase in heart rate. We believe that our results indicate individual differences (and possibly breed differences) in the sympathetic-parasympathetic balance.

Afferent impulses from the viscera may be relayed back to the cortex, evaluated there, and in turn produce an emotional response. This cyclical process is well known in human hypochondriacs. Its importance in animals has not been demonstrated.

If we were to summarize the view presented here we would say that the experimental situations stimulate the exteroceptors of the animal. The situation is analyzed in the cortex and two types of responses follow; the somatic response going through the motor cortex and other motor centers produces a pattern which is modifiable by training. In fact, a large part of training of a dog or a child involves the modification of the somatic patterns. By release of inhibition or by direct excitation, the hypothalamus stimulates the parasympathetic and sympathetic nervous systems leading to a characteristic visceral response pattern. This in turn, through interoceptors, may produce stimulation of the cortex, re-analysis, and continued emotional response.

We do not know very much about the occurrence of emotional reactions in animals under natural conditions. Judging from laboratory observations, one may be quite sure that external behavior is not always a reliable sign of internal visceral reactions with whatever psychological concomitants may be involved. Such knowledge is essential for an understanding of the effect of the emotional reactivity on social relationships between animals.

The Radio-inductograph. The radio-inductograph was developed as a tool to attack this problem. The device is still in a developmental stage and will eventually be more precise and convenient to use. In its present form, it can be used to investigate problems of the type discussed above. The following description of the radio-inductograph is modified from a paper by Fuller and Gordon.[6]

The device uses physiological activity as a means of modulating a radio-frequency signal. The signal is detected and amplified by a special receiver whose output appears as a d-c potential, which is proportional to the frequency of the signal over a range of about 15 kc. This output may be used with a power amplifier and penwriter or with a suitable oscillograph to produce graphic records. A diagram of the arrangement is shown in FIGURE 1.

There are four major components included in the system. Pickup units are of two types, pneumo-inductive and direct-inductive. The pneumatic pickups can be balloons, capsules sealed over an artery, or pneumographs. These are connected by heavy-walled tubing to the inducto-tambour, which is located in the transmitter. On the diaphragm of this tambour is a metallic foil ring, the movements of which alter the inductance of the coil and frequency-modulate the radio wave. We have made some use of direct inductive pickups in which the foil ring is moved directly by the respiratory or pulse movement and the coil is located outside the transmitter.

The transmitter is a simple, plate-tuned oscillator employing a 1S4 tube, with plate and screen connected so that it acts as a triode. Power is supplied from a flashlight cell and from two $22\frac{1}{2}$ volt miniature B batteries. The transmitter, with its batteries, measures $3\frac{1}{4}''$ x $3\frac{1}{2}''$ x $1\frac{1}{4}''$ and weighs $7\frac{1}{2}$ ounces. It fits into a pocket in the clothing or into a case attached to a harness on an animal.

The receiver uses twelve tubes, not including the power supply, and is designed to deliver direct current at a voltage proportional to the frequency of the signal. By this means, even though the distance of the transmitter from the antenna varies so that the strength of the signal received is changed, the output is not effected, provided the signal is strong enough to be detected. By providing for tuning, one can successfully tune in several transmitters on adjacent wave bands. Visual monitoring is provided by an electric eye, and auditory monitoring from a phone jack, connected to a special audio-frequency output.

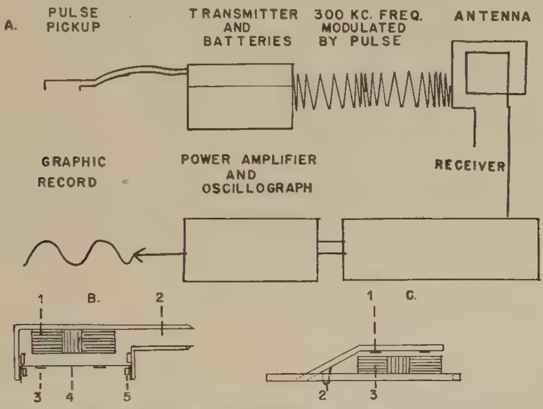
A.
PULSE PICKUP
TRANSMITTER AND BATTERIES
300 KC. FREQ. MODULATED BY PULSE
ANTENNA
GRAPHIC RECORD
POWER AMPLIFIER AND OSCILLOGRAPH
RECEIVER
1
B.
2
3
4
5
1
C.
2
3

FIGURE 1. (A) Schematic diagram of radio-inductograph system. (B) Cross section of inductor-tambour: 1, coil; 2, air inlet; 3, modulating ring; 4, rubber diaphragm; 5, split ring to hold diaphragm in place. (C) Direct pulse pickup: 1, modulating ring; 2, button placed on artery; 3, coil (Fuller and Gordon[6]).

The recorder may be of several types. We have used a Grass model III electroencephalograph with a special low-speed, paper-moving mechanism. The output of the receiver is plugged into the input board of the electroencephalograph and tuned, and, after amplification is adjusted, records can be made. Because of the relatively high input voltage, the preamplifier of the electroencephalograph is not used, and the receiver output is applied directly to the power amplifier.

FIGURE 2 shows some sample records which were made with this arrangement. From top to bottom, these records show human carotid pulse, made with a capsule applied over the artery; human pneumogram, with heartbeat superimposed; human finger pulse; and the dog's pneumogram, made with the animal moving about freely during the receiving of the record.

An example of radio-inductograph records from an actual experiment is shown in FIGURE 3, which reproduces records of three dogs trained in a delayed response. The animals were required to select the correct escape

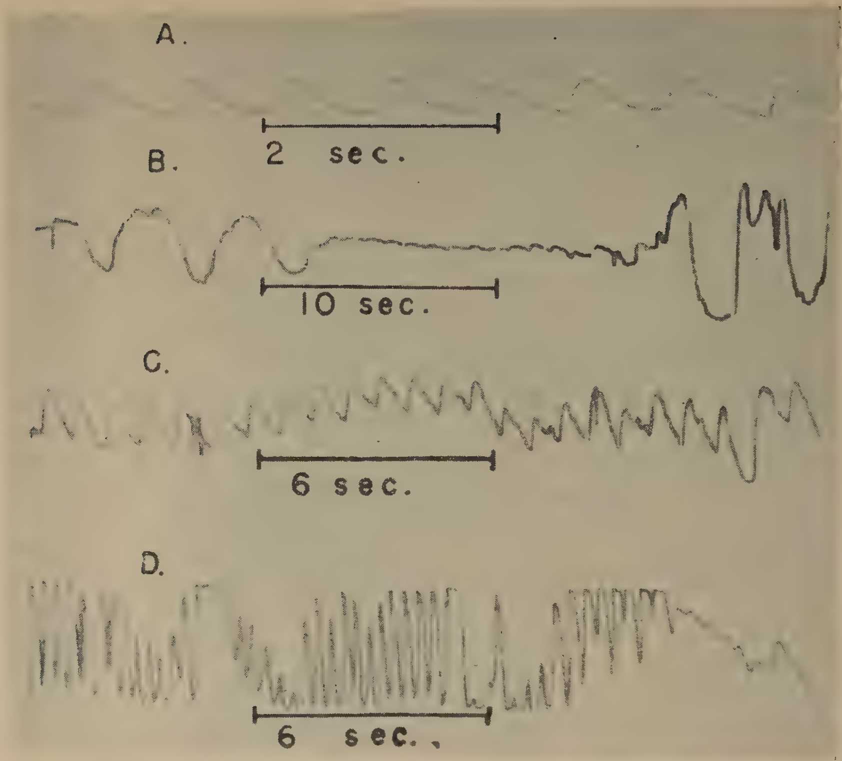

FIGURE 2. Sample radio-inductograph records. See text for description (Fuller and Gordon[6]).

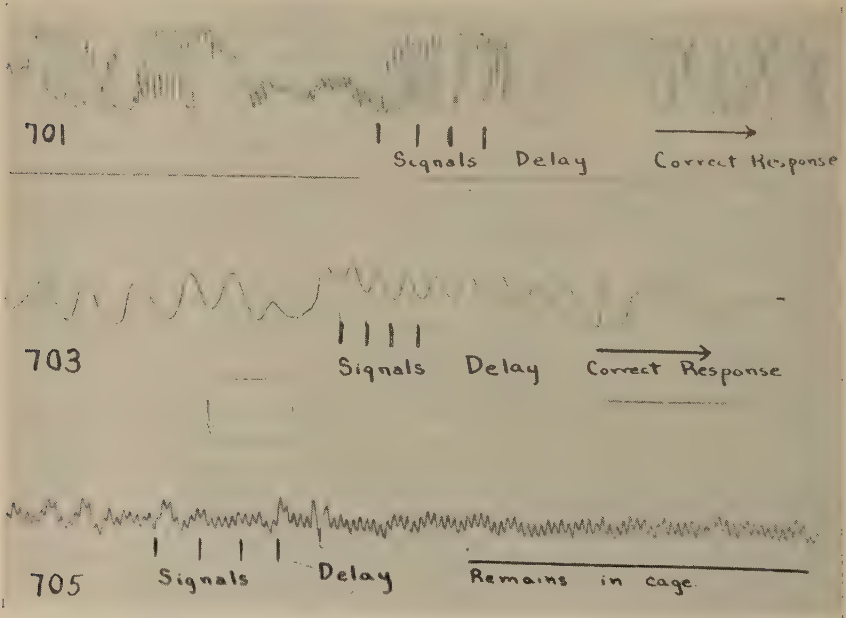

FIGURE 3. Radio-inductograph records of dogs during the delayed response test. See text for description.

door when the opportunity to respond was delayed for a period of 5 seconds. The upper record is from a highly successful animal (which mastered delays up to 60 seconds) and shows a slight, but definite, change in depth and rhythm at the time of the signal and during the delay. The middle record is from a less successful animal, who was limited to delays of 10 seconds. Respiratory changes of this animal are extremely marked. One may hypothesize that this animal was a little too reactive and became distracted during long delays. The bottom record is from an untrainable animal. His respiratory rhythm was unaffected by stimulus or delay, and he was completely unresponsive. The environment was more or less shut out from this subject and changes in emotional level necessary for adjustment did not occur.

What are the fields of usefulness of the radio-inductograph and what are its limitations? One important consideration is the ratio of the displacement to be measured compared with other displacements due to gross bodily movements. Thus, we can easily record respiratory movements of a walking or running dog. The body movements do produce distortion of the pneumogram, but, unless one is interested primarily in details of form, the distortion is welcome, as it provides a record of activity. We have not yet secured good pulse records from an active dog, although this is possible in man, whose surface pulse is stronger. In humans, we have obtained records of good quality during moderate activity, such as walking and speaking before an audience. An inflated cuff about the limb of the dog will transmit the pulse, but this arrangement is not desirable for a long-term observation during activity.

The amplifier system of the recorder we are using is not adapted for very low frequency response. With a suitable arrangement, however, there would appear to be no difficulty in recording from a gastric balloon. The limitations at this stage are not so much in the radio-inductograph as in the production of reliable mechanical pickups which will not hamper the animal.

Can other means be used to modulate the radio wave? It should be possible to employ changes in resistance and thus detect the galvanic skin reflex. With the use of additional tubes, it should be possible to utilize cardiac action potentials as modulators. Additional tubes increase weight and battery drain. We are now in the stage of determining the practicality of these and other possible arrangements.

The range of the instrument varies somewhat with condition. Using an antenna zig-zagged across an open field approximately 100′ x 25′, it was possible to obtain satisfactory records of respiration over the entire area. We have also used a large inside room and can obtain good records from animals free to roam about within it. A simple loop antenna tuned to the frequency of the transmitter will pick up very satisfactorily. One point which must be considered is the limitations of the Federal Communications Commission, which does not allow transmission from unlicensed operators above a certain minimum level. When adapted to animal or human subjects, the device is inconspicuous and does not hamper activity. It can be worn for considerable periods of time. Battery life with continuous operation is about 8 hours for the B battery and 4 hours for the A battery. With intermittent operation two hours per day, these lives are about twice as long.

The field of application of the radio-inductograph should fall between those of precise laboratory studies and field observations of absolutely unrestrained animals. We hope that by use of it we can increase our knowledge of the role of emotions in social adjustment in animals and in human subjects.

Summary. Animals show individuality in many aspects of behavior, particularly in the sphere popularly called emotional. Much progress has been made in the investigation of visceral responses to physical and social stimulation, and the central mechanisms involved are fairly well understood. Little is known of the occurrence of visceral responses in animals under natural conditions, or of the importance of such reactions as determinants of behavior. An apparatus, the radio-inductograph, has been devised to meet the needs of research on this problem.

The radio-inductograph uses physiological activity as a means of modulating a radio frequency signal. A pneumatic pickup is connected to a tambour containing the oscillator coil of a miniature transmitter. Movements of a foil ring on the tambour diaphragm alter the inductance of the coil and frequency modulate the R. F. signal. The receiver is designed to deliver direct current at a voltage proportional to the signal frequency and, within limits, is independent of signal strength. Thus, the subject may move about freely during a recording period. An oscillograph sensitive to low frequencies is used to produce graphic records of pulse, respiration, or other movements. The device is useful in situations where restraint of the subject would defeat the purpose of the experiment.

References

1. ARNOLD, M. 1948. An excitatory theory of emotion. Mooseheart—Univ. of Chicago Symp. on Feelings and Emot. (abstract).
2. BARD, P. 1948. Central nervous mechanisms for the expression of anger. Mooseheart—Univ. of Chicago Symposium on Feelings and Emot. (abstract).
3. CANNON, W. B. 1929. Bodily Changes in Pain, Hunger, Fear and Rage. 2nd Ed. Appleton, New York.
4. DUFFY, E. 1941. The conceptual categories of psychology: a suggestion for revision. Psychol. Rev. **48:** 177–203.
5. FULLER, J. L. 1948. Individual differences in the reactivity of dogs. J. Comp. & Physiol. Psych. **41:** 339–347.
6. FULLER, J. L. & T. M. GORDON JR. 1948. The radio-inductograph—a device for recording physiological activity in unrestrained animals. Science **108:** 287–288.
7. LIDDELL, H. S. 1942. Psychosomatic Medicine **4:** 309–395.
8. SCOTT, J. P. 1948. Studies on the early development of social behavior in puppies (abstract). Amer. Psychologist **3**· 239–240.

EFFECTS OF NUTRITION AND DISEASES ON EXPERIMENTAL ANIMALS

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Behavior studies have been conducted on many different animal species. Obviously, it is impossible in the space allotted to cover all of their needs, from a disease and nutritional standpoint. Hence, this discussion will be limited to the principal laboratory animals, such as guinea pigs, rabbits, dogs, cats, mice, monkeys, and rats.

Behavior studies are apt to be fairly long-term observations. Therefore, the origin of the animals and their care during experiments is important. In such studies, it is just as important to have standardized animals and standardized conditions for maintaining them as it is for the qualitative chemist to have standardized reagents and accurately calibrated equipment. Individual variations in animals are sufficient, without adding to the confusion by having irregular and improper feeding and management regimes.

It is axiomatic that the worker should understand normal behavior and appearance of the animals being used before behavior studies are instituted. Furthermore, this is essential before one can discern abnormalities due to discomfort or disease in the animals. Caretakers should be well versed in the appearance of and requirements for normal animals before studies are started. If need be, time should be allowed for the caretaker to become acquainted with his stock before experiments are begun.

Few laboratories are equipped specifically to care for all the many different types of animals that may be used. In most cases, however, the essentials for a given species can be supplied without great difficulty. In any event, cages should facilitate observation, allow freedom of movement for the animals, and permit cleaning and feeding without undue disturbance to the animals. In addition, animal comfort must be provided by supplying such things as bedding, retreat quarters, and facilities for carrying out the natural body processes according to the species being worked with.

In behavior studies in the field, the usual procedure is to report the number of animals observed and studied, their sex and age, food available, beds, indications of breeding, *etc.* In laboratory or confinement studies, such as might be conducted in a zoo, the same data should be reported, *i.e.*, size of quarters or cages, number of animals, food, frequency of feeding, age, sex, breeding activity, *etc.* There may be a tendency to overlook these things in laboratory studies. Too many times, it is taken for granted that these things are understood. In other situations, the worker himself does not conform to the accepted and now definitely determined optimum methods of quartering and feeding laboratory animals.

Nutrition. "Pigs is pigs" is not necessarily the case with laboratory guinea pigs. Their feeding and environment too greatly affects their behavior. For years now, there have been available prepared foods for the usual laboratory animals, and it is difficult to understand why certain workers in animal behavior ignore or refuse to take advantage of this and other available knowledge regarding feeding and housing laboratory animals.

Long ago, it became apparent to workers in physiology that it was necessary to work with normal animals. In order to have normal animals, it was apparent normal diets had to be developed first. Many published experiments had to be discredited after it was found that the results would have been different if a proper diet had been used during the experiments. Results already obtained could not be repeated when the newer knowledge of nutrition was applied. This conceivably could be true in experiments in animal behavior.

Granted, most workers do follow the accepted procedures for feeding and handling of animals in their behavior studies, but too many do not. This is bad enough but, when students in behavior are not instructed or informed as to the importance of nutrition and disease in their test animals, it is inexcusable. Too many times, experiments are misleading as a result of improper nutrition, or the experiment may be a failure because of loss of the animals by disease.

Adequate and optimum in nutrition are not necessarily synonymous. Animals may live and appear to be healthy and normal on a seemingly adequate diet, but the diet may not be optimum; hence, reproduction or some other normal process may be limited. When the so-called "deficiency diseases" were discovered, pathology came into the picture, and it became important to distinguish between physiological abnormalities resulting from diet and abnormalities caused by infectious diseases. As an example, abortion may be caused by deficiencies in diet or by infectious agents. In such a case, neither possibility should be neglected.

While slaughter experiments are more costly, time-consuming, and not always practical in field studies, they are the only true check on a study. In each study, a sufficiently large number of the animals studied should be destroyed and examined at the close of the observation to minimize the rather large individual variability in composition.

The behaviorist must have an appreciation of the points at which nutrition and pathology touch his primary field of interest. He must recognize, also, the role of inheritance.

The term, growth, indicates a characteristic growth rate for each species and a characteristic adult development and size. True growth involves an increase in the structural tissues of muscle and bone as well as all the organs. Heredity fixes the potential maximum size and development. An essential factor determining whether this maximum will be reached is nutrition, and only an optimum nutritional regime will enable an organism to take full advantage of its heredity. Maximum development is fixed by heredity, and the normal organism cannot exceed it through nutrition or any other means.

Diets for the usual experimental animals are well standardized and readily available commercially. We will not go into detailed descriptions and formulae of diets for different species. A diet of natural food materials which is satisfactory for the rat probably will also amply provide for the cotton rat and hamster. Guinea pigs and rabbits fail to grow and survive on diets which are satisfactory for rats. Certain known effects of deficient diets will be brought out. The rat has been the subject of more nutritional studies than any other experimental animal. However, the requirements of all the principal laboratory animals are now quite well understood.

Proteins are required for the formation of new tissue during growth, the synthesis of such secretory products as milk, and replacing tissues catabolized during normal metabolism. This is reflected in the production of more and larger litters and the most satisfactory lactation in rats on a high protein diet. A diet containing 25 per cent protein seems to be the optimum for rats.[1] This may vary with different strains of rats.

Fat-low diets result in dermatitis, renal degeneration, growth failure, irregular ovulation and failure of males to breed, lowered lactation,[3] and resorption of fetuses or prolonged gestation with frequent maternal mortality and death of newborn.[4]

Vitamin A deficiency results in both abnormal osseous development and soft tissue growth failure,[5] female sterility,[6] and functional failure of glands.[7] A disproportion between soft tissue development of the central nervous system and the skeletal system in rats results in nervous manifestations due to pressure effects.[8]

Vitamin D and its relation to calcium and phosphorus in rickets is quite well understood. Certainly, an animal with severe rickets, semi-immobilized with soft bones, is going to develop secondary muscle atrophy and will be a poor specimen for behavior studies.

Vitamin E is concerned with reproduction and muscle dystrophy.

Thiamine deficiency is reported to be associated with degeneration of the nervous system, polyneuritis, muscle atrophy, cardiac dysfunction, and anorexia.

Neurological abnormalities with peripheral nerve myelin degeneration and degeneration of the posterior columns of the spinal cord follow prolonged subsistence on diets low in riboflavin.

Pantothenic acid deficiency is reported to result in specific neuropathologic changes in the spinal cord in chicks[9] and nerve degeneration in pigs.[10]

Pyridoxine is essential in the diet of rats, dogs, pigs, and poultry. Deficiency of pyridoxine produces such things as uniformly defective sexual behavior and convulsive seizures in rats suckling dams on pyridoxine-deficient diets.[11]

Rats reared from weaning on calcium-deficient diets have failed to mate, while mothers on calcium low diets do not lactate normally.

Rats placed on magnesium-deficient diets, two to three days after weaning, become nervous and hyperirritable. As the deficiency progresses, the animals become weak, less irritable, and listless.[12]

In uncomplicated potassium deficiency, rats show extreme alertness, marked pica, delayed sexual maturity, and irregular and delayed ovulation, with occasional cessation of estrus.[13]

Iodine and its effects upon the thyroid needs no comment.

Disease. There are certain diseases commonly occurring in animal groups that can be avoided by cognizance of the diseases and the use of principles of nutrition, management, preventive medicine, sanitation, and disease prophylaxis. Such diseases may be entirely nutritional, viral, bacterial, or parasitic in etiology. Respective examples are suckling pig anemia, canine distemper, panleucopenia in cats, Pasteurella infections, and "stomach worm" disease of sheep. Obviously, sick animals are not going to reflect normal behavior. Sick or undernourished animals are not going to have normal breeding cycles nor are they going to conceive and raise their young.

Without employing vaccination for canine distemper and "cat plague," dog and cat colonies cannot be maintained. Paratyphoid infections may wipe out guinea pig colonies. Ectoparasites, such as Otodectes ear mites, may be so annoying to rabbits that they may lose condition and emaciate to the point where secondary infections develop which result in death.

Paratyphoid infection or Salmonellosis is one of the most frequent diseases occurring in animal colonies. Guinea pigs, rats, mice, birds, rabbits, reptiles, monkeys, and dogs, in fact, all species, are susceptible. The natural hosts, if such can be declared, are wild mice and rats. Carriers of this disease are common and may not be known until the resistance of the stock is lowered through such things as dietary deficiencies, chilling, and reproduction, which permit the onset of an epidemic which frequently results in a high mortality rate. Such occurrences may develop at any stage of an experiment and result in the total loss of an otherwise successful study. Paratyphoid carriers introduced into an otherwise clean and well-established but susceptible stock can cause disastrous results. Infected colonies are best done away with in their entirety. A simple routine of stool cultures will detect carriers and should be depended upon to maintain a clean colony and screen out infected new animals that might be added to the existing stock.

Tuberculosis is of principal importance in primate collections. It can, however, be prevented by systematic testing and isolation of all animals acquired. The importance of this is evident from statistics which show that the incidence of the disease in newly imported animals may run as high as 25 per cent. Periodic testing of the animals and examination of personnel are mandatory if the disease occurs. Experiments should be set up in sufficient time to provide an acclimatizing period for the animals and to prevent them from becoming sick after the experiment has started.

Behavior is generally known to be closely associated with hormones, the product of glands of internal secretion. They, in turn, are bound to be influenced by nutrition. To be sure, there are basic patterns for hormonal activity which cannot be deviated from beyond the potential maximum and minimum, but these extremes can be effected by nutrition and disease. The effects of nutrition on hormonal behavior patterns is in itself hard to predict because of the mere complexity of the interdependability of the various glands of internal secretion. This brings up again the value of "slaughter or sacrifice" experiments. Hypo- and hyper-activity of the endocrine glands most directly responsible for the particular behavior being studied should be examined and recorded at the conclusion of the study being reported.

Several points should be emphasized in closing. Those whose primary field is pathology, nutrition, or physiology, rather than behavior, can profit tremendously from the studies of behaviorists. This can best be accomplished by the behaviorist reporting his experiences with nutrition and disease in his animals. Behavior studies can be more properly evaluated if the reports of such studies include a description of the animals used as to strain, source, age, sex, quarters housed in, feed used, the presence or absence of disease, and mortality, growth, and reproduction rates during the studies. Both graduate and undergraduate students should have a full appreciation of the sciences intimately related to their primary field.

Summary. Certain basic principals of animal nutrition, methods of feeding, and types of feed available for the common laboratory animals are discussed. The importance of proper nutrition for experimental animals is stressed. Some examples of the effects of inadequate or improper nutrition on experimental animals are given. Disease conditions commonly occurring in laboratory animals are described and methods of prevention and treatment presented. It is urged that all publications reporting studies of animal societies include a description of the animals studied as to strain, source, age, sex, quarters housed in, feed used, mortality, growth and reproduction rates, and the presence or absence of disease during the studies.

References

1. McCoy, R. H. 1940. Effects of different levels of protein in the diet of the rat. J. Biol. Chem. **133:** lxiv.
2. Burr, G. O. & M. M. Burr. 1929. A new deficiency disease produced by the rigid exclusion of fat from the diet. J. Biol. Chem. **82:** 345–67; *idem.* 1930. On nature and role of fatty acids essential in nutrition. J. Biol. Chem. **86:** 587–621.
3. Maynard, L. A. & E. Rasmussen. 1942. Influence of dietary fat on lactation performance in rats. J. Nutr. **23:** 385–98.
4. Evans, H. M., S. Lepkovsky, & E. A. Murphy. 1934. Vital need of body for certain unsaturated fatty acids. J. Biol. Chem. **106:** 431–50.
5. Mellanby, E. 1938. The experimental production of deafness in young animals by diet. J. Physiol. **94:** 380–98.
6. Evans, H. M. 1928. The effects of inadequate Vitamin A on sexual physiology of the female. J. Biol. Chem. **77:** 651–54.
7. Wolbach, S. B. & E. Howe. 1925. Tissue changes following deprivation of fat-soluble A Vitamin. J. Exp. Med. **42:** 753–77.
8. Wolbach, S. B. & O. A. Bessey. 1941. Vitamin A deficiency and the central nervous system. Am. J. Path. **17:** 586.
9. Phillips, P. H. & R. W. Engle. 1939. Some histopathologic observations on chicks deficient in chick antidermatitis factor or pantothenic acid. J. Nutr. **18:** 227–32.
10. Wintrobe, M. M., J. L. Miller, Jr., & H. Lusco. 1940. Relation of diet to occurrence of ataxia and degeneration in nervous system of pigs. Bull. Johns Hopkins Hosp. **67:** 377–405.
11. Patton, R. A., H. W. Karn, & H. E. Longenecker. 1944. Studies on the nutritional losses of normal behavior in albino rats. IV Convulsive seizures associated with pyridoxine deficiency. J. Biol. Chem. **152:** 181–93.
12. Sullivan, M. & V. J. Evans. 1944. Nutritional dermatoses in rats: evaluation of interrelationship of magnesium deficiency and deficiencies of Vitamin B complex. J. Nutr. **27:** 123–39.
13. Orent-Keiles, E. & E. V. McCollum. 1941. Potassium in animal nutrition. J. Biol. Chem. **140:** 337–52.

A STUDY OF THE PHYLOGENETIC OR COMPARATIVE BEHAVIOR OF THREE SPECIES OF GROUSE

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The methods and techniques used in this study had their beginnings many years ago. In working on the experimental embryology of one of the marine annelids, *Amphitrite*, the author learned the importance of keeping accurate records—giving the date, the hour, and even the fraction of a minute at which the observation was made. Later, in planning experiments on the life histories of parasites and parasitic diseases, the necessity of carefully prepared plans and the need to carry them through to a consistent conclusion received additional emphasis. Before one can make well-organized plans, exploratory surveys or observations must be made. All this was true in the present study. Another set of circumstances led to the studies on which this paper is based.

In 1939, the writer had not seen the mating of the sage grouse; in fact, he knew only two people who had seen such matings. Some declared they did not mate. One ranchman had observed the annual gathering on his place for forty years and had not seen mating, but said he learned in the old country how it was done: the cocks in strutting coughed up the sperm, and the hens later came along and picked it up while feeding. Variations of this myth were common among residents of the sage grouse country.

While this ignorance was amazing, an inspection of the literature was equally disappointing. Bailey[1] had accepted the explanation by Frank Bond, that the breast feathers of the cocks were worn off, exposing the large bare spots, by sliding on the ground after the air pouches were filled ("Auk," 1900). It was startling to find that neither the mating nor the mating cycle had been described. Practically nothing was known of the social relationships or the life history of the largest (with one exception), native, upland game bird of North America. This ignorance of the social behavior was exceeded only by ignorance of the relationship of this bird to its environment, the necessary basis of any rational measures for the preservation of the species.

Observations on the sexual cycle of the sage grouse began in 1940. The main features of the early study were published in 1942.[2] The first year, six strutting grounds were located. Enough information was gathered to show need of a better organized plan. The next year, an area was chosen on which the largest number of birds had been found. Besides several daytime trips, fourteen nights were spent on this area. Observations on the prairie, sharp-tailed grouse were made in 1947 and 1948. Observations on the greater prairie chicken were made in 1948.

Ordinarily the birds congregate for two daily assemblies, one in the evening, and the other, the larger, more significant assembly, at daybreak the next morning. In order to avoid any serious disturbance of the birds, it was customary to go out in the afternoon, set up my tent at a convenient spot, and go inside before any birds appeared. Usually, I did not come out of the tent until all the birds left the area. The hour and minute of all observations were recorded and notes were taken, to be expanded later. A movie camera, equipped with a four-inch or a six-inch telephoto lens, was used to record behavior. Kodachrome film was used. At night, a convenient flashlight, a watch, a notebook, and pencil were kept handy to record observations at any hour.

This study embraces observations during the mating cycle of representatives of three closely related genera of the family *Tetraonidae: Tympanuchus*, *Pedioecetes*, and *Centrocercous*. The species studied were the greater prairie chicken, *Tympanuchus cupido americanus* (Reichenbach), the prairie sharptailed grouse, *Pediocetes phasianellus campestris* (Ridgway), and the sage grouse, *Centrocercous urophasianus* (Bonaparte). As with other *Tetraonidae*, the hind toe is short and raised above level of the front toes, the leg is without a spur, the head is feathered, the tail is not vaulted as in the pheasants, and the plumage is nonmetalic. In the three genera considered, the leg is feathered down to the base of the toes. *Centrocercous* is distinguished by narrow, pointed, tail feathers, while the other two genera have the tail feathers broad and rounded. In *Tympanuchus*, the sides of the neck have prominent tufts of feathers. In *Pedioecetes*, the tail feathers are graduated in length, the middle ones being much the longest; hence, the name, "sharptail."

One internal structure is of particular interest. In all three species, the oesophagus of the males, as the mating season approaches, develops greater elasticity, so that it may be expanded into air sacs of characteristic form and size. These air sacs are used to make sounds that are apparently intended to attract the attention of females or to challenge a rival. The air sacs, combined with action of adjacent external, muscular, dermal, and epidermal structures, play an important part in the sexual behavior of the males. The action and the resulting behavior in each species, however, are strikingly different.

In relation to their environment, the range of the prairie sharptail lies almost entirely within the former range of the greater prairie chicken except toward the northwest, but it does not extend so far south or so far east. The former range of both these birds overlapped or bordered on the eastern range of the sage grouse.

Characteristic of all three species is the fact that they use the same strutting areas year after year, "ancestral" in the sense that they are used through successive generations. In one instance, the location of a sage grouse strutting ground persisted many years after a public graded road was put through the area. When used by prairie chickens, such areas are commonly called "booming" grounds; used by sharptails, such an area is frequently called a "crowing," "dancing," or "parade" ground; and, when used by sage grouse, such areas are best called "strutting" grounds, due to the pompous, fantastic strut of the males. All such areas are on open hillsides or plains and are usually so situated that all parts of the area can be seen from any one location within the border.

Annual Assemblies. The three species of grouse studied have the sexual cycle at about the same season of the year. In all three, the cocks appear in the spring on the strutting grounds earlier than the hens and continue the daily assemblies later than the hens. The annual courtship cycle lasts ten weeks or more. In the late spring of 1948, the height of the mating season of the prairie chicken at 3,200 feet elevation was about the middle of April. It occurred about one week later in the sage grouse at an elevation of 7,100 feet, where snows were still common. In the sharptail, it was not reached until near the middle of May. In the sage grouse, the daily assembly of cocks begins late in March and continues, unless interrupted by severe weather, into June.

Daily Assemblies. In general, weather permitting, there are two daily assemblies, one in the evening and one in the morning, at which mating occurs. Sage cocks may begin to assemble by walking into the area as early as five o'clock in the afternoon, but usually not before six p.m. or near sundown and not at all in very severe weather. The prairie chicken cocks begin to assemble early in the afternoon on fine days and, depending on the weather, later or not at all. The sharptails have been seen on the area at midday, or, if they left the area in the morning, they may reappear within an hour or at any time during the day. Both prairie chickens and sharptails leave the area while there is still considerable light in the western sky. Some sage cocks stay until almost dark before they fly away. As the new moon approaches full, some birds remain on the area all night. At the height of the mating cycle, some hens wander about in the full moon, but I have seen no indication of mating at night. Only two matings of the sage grouse have been seen at the evening assembly about half way between sundown and dark. No indications of mating at the evening assembly have been seen in the other species.

All three species come very early to the morning assembly, the sage grouse at the first break of day, the prairie chickens and the sharptails a few minutes later. Strutting and other activities increase and usually reach a peak in 30 to 40 minutes. By this time, hens are present and the organization of the cocks for the morning is pretty well established. The hens begin to leave 30 minutes to two hours before the cocks do. All mating, with a few exceptions in the sage grouse, occurs during the morning assembly, much of it before sun up; fully fifty per cent of sage grouse mating takes place before that hour.

Mating Behavior. No attempt was made to evaluate the specific or even relative importance of heredity and environment on the social behavior. It has been said that the inside of an animal shows its phylogenetic relationship, and the outside structures show where it has been—the adaptations or influence of environment. The organism does not exist apart from its environment, however, and structure does not exist apart from function. Since behavior can be roughly defined as the reaction of the organism to external and internal environment, or to both, and since internal environment is determined in part by structure, no attempt is made here to separate genetics and environment as causal factors of social behavior. No doubt, one or the other factor sometimes plays a major part in certain types of behavior. Since identical or homologous structures are accepted as indicating close phylogenetic relationship, however, for the purposes of this paper, we have regarded identical or closely resembling behavior as primarily of genetic or phylogenetic origin.

Morphology and Behavior; Functions of Air Sacs. Let us illustrate by two types of behavior, both used by the males to attract females. In all three species, the throat or oesophagus, of the males with adjacent structures, is so constructed that it may be more or less enlarged in the form of air sacs on the sides of the neck during the breeding season. In the prairie sharptail, the air sacs, when expanded, are hemispherical and comparatively small in size, and the sides of the neck are covered with enlarged feathers. While the air sacs are being inflated, these feathers raise and expose a hidden patch of reddish, distensible skin. The cock stretches out its neck, forces air into the air sacs, usually two or three respirations in succession, and in so doing emits a low "coo-o, coo-o." The air sacs appear to act as resonators. This sound serves to challenge a rival perhaps more than to attract a female.

In the prairie chicken, the expanded air sacs are bulb-like and much larger in size. On each side of the neck is a long black tuft of feathers which covers the highly inflatable air sac, which during the breeding season is reddish (or later orange-yellow) in color. In preparing to boom, the greater prairie chicken stretches its neck, directs the tufts of feathers forward above the head, and fills the air sacs with a few forced respirations. It then gives the characteristic booming sound. Close at hand, this sounds to the author like "oOM-VOOM-VOo," with the accent and volume on the second syllable. This booming sound is the chief mating call used to attract females to the booming grounds. It is also one of the means used to challenge a rival.

In the sage grouse, the very elastic air sacs are grotesquely enlarged during the breeding season, the enlargement extending from one to the other across the ventral side of the oesophagus. At the same time, the skin of the entire breast becomes highly distensible and elastic. The sage cock can swallow air into its oesophagus, and usually does, before it begins the strut. When about to strut, the cock takes a few steps forward in a quarter circle, throws back its head, and takes a full breath. Then, with violent pumping action in which the wings are raised and lowered two or three times, he fills the air sacs to maximum capacity with forced respirations, and, without any audible sound, except one made by rubbing the wings lightly against the breast, forcibly expels the accumulated air through the nostrils with a sharp whistle-like "purp," followed immediately by a dull "plop," made by the complete collapse of the large air sacs. This performance is repeated frequently, before and as long as any hens are in the area, with the evident purpose of attracting their attention. At other times, the action is used as a challenge to a rival, or simply as a means of liberating pent-up energy. When the air sacs are expanded, two large yellowish or grayish white bare spots are exposed, which are surrounded by short stiff feathers bordered with longer ones. When the air sacs are contracted, the bare spots are completely covered by the surrounding white feathers.

From this description, it is clear that one structure with different degrees of development, the oesophagus, is capable of producing a variety of behavior, most of which is concerned with social relations of the sexes. Sounds are produced in each species, but in different ways. This type of behavior is primarily based on structure, and some similarities in performance indicate a probably phylogenetic significance.

Environment and Behavior. Let us examine another type of behavior on which environment seems to have had a major influence. Soon after it comes on the booming ground, the cock of the greater prairie chicken, along with occasional booming, has the habit of jumping high in the air, clapping its wings rapidly, and cackling loudly. I have noted jumps from 15 inches to 6 feet in height, and from 0 to 48 feet in length. Most of this type of behavior takes place on the strutting area, and before it is light enough to take Kodachrome pictures. After sun-up it becomes infrequent. Since the booming sound is so deceiving as to distance and comes from different directions, this jumping action is useful in the high grass country to direct the hens by movement and sound to the center of the booming area where mating occurs. A good deal of cackling continues after most of the jumping stops.

Similar behavior, but more limited in cackling and in the number and size of the jumps, is found in the males of the prairie sharptail, at the same time of day. There is a good deal of cackling while running about on the ground. In this species, the jumping appears to be as much for the purpose of releasing energy as for attracting the females. It should be noted that the chief habitat of the sharptail is in the short grass country, where such behavior would not be so important in attracting the females and where the view is not obstructed by tall grass.

I have seen sage cocks, more frequently the younger birds, jump into the air and clap their wings, but otherwise making no noise. The action appeared to be the exuberance of living, usually occurred after the hens left the area, and certainly had no influence in attracting the females. Ornithologists rank the three genera listed in this study in immediate sequence, indicating close genetic relationship. If the ancestors of the sage grouse ever had the habit found in the greater prairie chicken, it has long since vanished. It is certain that the sage grouse has a much more highly specialized social organization than either of the other two species studied. It would seem that the habit of jumping and cackling early in the morning arose as a response to environment, rather than having any structural significance.

Social Organization. (1) *The Greater Prairie Chicken.* One trip for study of the greater prairie chicken was made April 2, 3, and 4, 1948, about 16 miles north of Ogallala, in west-central Nebraska. The time proved to be too early for the mating season, and no hens were seen on this trip. On April 2, the weather was windy and partly cloudy. Only a few cocks came into the area and these were disturbed by the sight of the tent. The next morning, a total of 13 cocks were seen and all left at 6:55 a.m. In the warm afternoon of April 3, the first cock boomed west of the tent at 3:50 p.m. Gradually, others came in, but there were warning signals and 9 cocks flew away at 4:47 p.m. By 5:10, the birds were coming back, and by 5:35 p.m. most of the booming was within the central strutting area. A few minutes later, the sky clouded up, the wind began to blow, and the last of the cocks flew away at 5:42. At 4:00 a.m. on April 4, the sky was bright and clear. The first booming was heard north of the strutting ground at 4:18 a.m. Twenty minutes later, booming and quarreling were common, and at 5:00 a.m. 13 cocks were counted. Cocks left at 6:53 a.m.

Very early in the morning, booming at a distance is heard. As cocks come to the booming ground, challenging or quarreling sounds begin and they continue all during the morning assembly, gradually diminishing. There is a limited area occupied by a cock or pair of cocks, but no specific spot, as is usually the case in the sage grouse. At this early season, there appeared to be no real fighting. In booming, the cock patters the ground with his feet very rapidly for two or three seconds, lowers his head and stretches his neck, erects and directs forward above the head the black tufts of feathers on the sides of the neck, pumps air into the bulblike "drums" on the sides of the neck, and makes the booming noise previously mentioned. The cock then straightens up and looks around or runs forward several steps. He may boom several times in succession. As the cocks gather on the central strutting or mating area, they have the habit of jumping in the air, clapping the wings, and cackling with a loud "qua, qua, qua, qua, quee, quee." Early in the morning the cocks move about a great deal and, in contrast with the sage grouse, do not appear to have any fixed place to strut. Later, there is not so much wandering movement, and the cocks get together in pairs. This is also a loose relationship, however, for they frequently separate in a short time and each challenges another cock. In this respect, they are much like the sharptail grouse.

When a pair of cocks approach each other, they usually squat low and chatter, as though challenging or scolding, and there appears to be a lot of bluffing. Then one will stand up slowly and, if the other makes the slightest move, the first cock will drop back on guard. After repeating this several times, one bird will rise, walk slowly away, and begin booming again. Early in the season, they make many passes but seldom come into bodily contact. While this appears more like bluffing than anything else, they seem to be satisfied after such a performance, and each one usually goes his way.

Other observations were made April 16, 17, and 18, during the height of the mating season. On a clear warm day, the cocks begin to come into the area early in the afternoon. This behavior is in contrast with the late afternoon arrival of the sage grouse and with the sharptail grouse, which may come back within an hour after they leave the morning assembly or at any hour during the day. In the morning, the booming usually starts a long way off. The earliest hour recorded was 3:50 a.m. on April 18. Most cocks come walking into the area, booming occasionally on the way.

(At this visit, the birds showed much less fear of the tent than before the mating season began.) The hens begin to come into the area some 20 to 40 minutes after the first cocks appear. A hen will stop here and there near where some cock is performing, apparently indifferent to what is going on; but, if about ready to mate, she soon drifts into the more centrally located mating area. As pointed out by Levi Mohler of the Nebraska State Conservation Department and verified by my personal observations, this mating area was 30 to 50 feet in width and 70 to 80 feet in length, much larger than the restricted mating spots of the sage grouse, where the hens gather in compact groups. In this area, there were three cocks, one of which appeared to be dominant. Mating did not take place on any particular spot within this area. When ready, the hen squats, the master cock rushes forward and mating is over very quickly. Quick as it is, however, the master cock is usually attacked by the nearest rival cock or cocks, and a bitter fight ensues. Similar sexual behavior is exhibited by the prairie sharptail, in striking contrast to the deliberate, pompous behavior of the sage cock, which is seldom attacked or disturbed even by his closest rival.

A summary of the social organization of the prairie chicken, on the strutting area, follows. The cocks usually walk into the strutting area, beginning the booming at a distance. As the cocks arrive, they take up accustomed positions scattered over the area. The territory covered by each cock is not narrowly limited, so that they may wander about while booming, sometimes going considerable distances to challenge another cock. The chief activities are booming, jumping in the air with loud cackling and clapping the wings, running about, bluffing, scolding, quarrelling, and some fighting. On one warm clear morning, the height of cock activity was reached at 4:18 a.m., as the hens arrived. Unless anxious for mating, the hens do not come into the area until all cocks are assembled. By this time, the cocks have settled their claims to certain territory.

Somewhat centrally located is the mating area, which is larger in size than the mating "spot" of the sage grouse. If not ready for mating, the hens wander over the area, stopping occasionally in the neighborhood of a booming cock, with adjacent cocks gathering around. If about ready for mating, the hens very soon wander into the mating area, where the master cock and two or three more dominant cocks are located. Here, the final contest in booming and strutting takes place, and the master cock mates with the waiting hen. After successful mating, the hen usually preens, waits around a few minutes, then leaves the area. After all hens leave, booming lags and stops, rivals renew their bluffing, quarreling, and occasional fighting. One pair noted fought about every fifteen minutes all morning. All activity gradually subsides.

The social relationships of the greater prairie chicken during the mating cycle are more primitive and not so highly organized as in the sage grouse. There is no definite hierarchy of dominance among the cocks, except the master cock, and he has to fight repeatedly to maintain that dominance. The boundaries of the territory occupied by a single cock are changeable and indefinitely established. The hens have the tendency to seek out the location of the dominant cock, which is true in the other species.

(2) *The Prairie Sharptail.* The social organization of the prairie sharptail during the sexual cycle is quite similar in many respects to the prairie chicken. Certain social relations show a higher degree of specialization. Territorial relationships of individual birds are more definitely established, and, under certain conditions, there is a well-organized drill or dance, led by the dominant cock.

Like the sage cock, the male sharptails walk or fly into the strutting ground before putting on any demonstration. Occasionally, calls are made as they approach the area. As the cocks assemble, they take up their usual stations, which are relatively fixed. Like the prairie chicken, however, the cock moves about considerably and may travel some distance to challenge a rival. Before the hens arrive, there is a lot of dancing, noise making, quarreling, and some fighting. In fact, one may spot the approximate location of the master cock by finding where the most feathers have been lost.

The dancing is unique. The cock lowers the head, stretches the neck, inflates the air sacs, coos, spreads the wings on a level with the body, and runs forward in a quarter or half circle with rapid mincing steps, all the time making a noise like the "putt, putt, putt, putt," of a distant motorcycle. He pauses, straightens up, makes a few challenging sounds, a sort of "cha, cha, cha," and repeats the dance. Before and while hens are present, there is at times remarkable group coordination in dancing, led by the master cock. After repeating the motorcycle dance for fifteen or twenty seconds, the whole group suddenly stops and is very quiet for a time averaging about ten seconds. During this period there is absolute stillness on the area, and other birds, like the meadowlark, can be heard clearly a quarter of a mile away. During this time, the cocks are like statues, alert to any sounds or sight of approaching hens. The whole performance is apparently led by the master cock. On the comparatively small area at the Custer Battlefield National Monument, all cocks took part. On the strutting ground near Moorcroft, Wyoming, where the birds were more widely scattered, only the cocks comparatively near danced in unison with the master cock. There is no such synchronized activity in the other two species studied.

Two other types of cock behavior are characteristic and related to rivalry. Dominance is primarily determined by vicious fighting between cocks. Both wings and beaks are used in rapid interchange of blows, too rapid for the eye to see. Feathers are frequently pulled out. The battles begin suddenly and continue for some seconds without pause. Sometimes, after a brief pause, the fighting continues as viciously as ever. After two or three rounds like this, one cock gives up, turns, and runs to escape, as rapidly as he can, pursued by the victor, who continues to peck at the vanquished even in pursuit. I have seen this pursuit extend 100 feet or more. By this time, other cocks join in the pursuit and the victim may be chased out of the area, the victor in the meantime returning to his accepted location.

A kind of gang fighting also occurs when the master cock attempts mating. As the master cock mounts the hen, he is always attacked by one, two, or three other cocks. So rapid is their action that, before a quick copulation can take place, the master cock is hit hard and sometimes displaced. A short fight ensues which usually results in the withdrawal of the attacking cock to a safe distance.

A milder sort of rivalry occurs in which there is usually no fighting and in which the cocks are grouped in pairs. There is a good deal of scolding, threatening chatter, bluffing, and watchful waiting. Two cocks approach (one usually runs up to the other) and stand facing in threatening position; then, alert, they squat low on the ground facing each other, with wings outspread and tense in every muscle. If one makes a quick movement as if to attack, the other responds instantly in similar manner, and both utter defiant "cha, cha, cha's." After repeating this several times, the pair frequently settle down for several minutes in watchful waiting. Should one start to leave, he quickly returns if the other shows signs of attack. If a third cock approaches the pair, one of the two cocks turns away and advances to challenge the third cock by uttering coo's, challenging calls, or performing the motorcycle dance. After a time, these apparently forget all about how it started, separate, and frequently the second cock returns to take up his vigil with the first cock. Later, these two separate by mutual consent. This kind of pairing off occurs most frequently while no hens are on the area, *i.e.*, at the afternoon assembly and after the hens leave in the morning.

The fierceness of competition for mating is shown by the following notes. On the morning of May 14 at 5:10 a.m., a hen appeared on the area and stopped at a place near the master cock. Four or five other cocks gathered around and the master cock fought and drove some of them back; the others did not come too close. By a slight flutter of her wings the hen indicated she was ready to mate. At intervals, this action was noted two or three times. At 5:15 o'clock, the master cock started to mate with the hen, but he was attacked by another cock and the mating was not complete. A fight resulted. At 5:28 the hen squatted and the master cock started to mate but was interrupted by other cocks. Again the master cock fought off the leader of the attack. Finally, at 5:30 a.m., a quick, apparently successful mating was made. Again he was attacked by two or three cocks which all struck him about the same time, and he then fought with two of them in turn.

After the hens leave, commotion among the cocks gradually quiets down, and they do a good deal of feeding, some preening, and rather quiet challenging in pairs. On the morning mentioned above, the last hen left at 6:20, but the last cocks did not leave until more than two hours later.

(3) *The Sage Grouse.* In the sage grouse, as in the other two species, the chief activities on the strutting grounds center around *rivalry for dominance* among the males and *competition of the males to attract or win the attention of the females.* Rivalry is settled chiefly by fighting and bluffing. Competition to attract females is accomplished mainly by strutting, in

which the enormously inflated air sacs, the large pendulous white breast, and the widespread tail play important roles. Since this performance has been described elsewhere, the social organization on the strutting grounds will here be briefly summarized. In this study, more than 350 cocks were scattered over an area one-third mile in length and averaging over 200 yards in width. There were only five small mating spots on this whole area. Except around these mating spots, the cocks were scattered widely, singly or in pairs, each cock or pair ready to protect, by fighting if necessary, its own territory, which was not always clearly defined. Individual cocks frequently challenged and occasionally fought with an adjacent cock. The pairs occasionally quarreled and fought, but did not separate. There was always more quarreling and bluffing than fighting.

The key to the social organization was found at the mating spot, which is constituted as follows. First there is a compact group of hens. At the peak of the mating season, 93 hens have been counted on one spot measuring about 15 by 20 feet. Strutting among the hens is the dominant or master cock, which does a large share of all mating (74 per cent, according to record). Usually there is a sub-cock or chief rival of the master cock, which also struts among the hens but is not allowed to mate except late in the morning and late in the season, after the master cock is sated. I have counted as many as 24 matings by the master cock in one morning. Sometimes, the master cock appears sated, but fights other cocks which attempt to mate. Surrounding this group is a fringe of from three to six males, best known as guard cocks, for these fight off any outside cocks that attempt to break into the inner circle. If the guard cocks approach too near the hens, they are driven back by the master cock or by the sub-cock. Vicious fights are frequent between the master cock and the guard cocks. Wing fighting is the rule, in which one cock attempts to strike the head of the opposing cock with a blow of the wing. On only two occasions have I seen a cock use the beak to seize the other cock by the back of the neck near the head and push him along for several yards out of the way.

In contrast to the other two species, the master sage cock is seldom disturbed while mating. If mating is not proceeding to suit the sub-cock or one of the surrounding cocks, one of them may attack the master cock and a fight ensues. I have never observed the result unfavorable to the master cock.

Dominance is well established, and has a lot to do with the ordinary procedure of mating. On a mating spot on which the hierarchy of dominance as described above is well established, mating goes on as an orderly procedure with few disturbances. On a temporary or newly established mating spot, which happens under certain circumstances, where by chance an isolated cock has attracted a group of hens, sometimes six or eight other cocks gather around to dispute dominance. There is a lot of quarreling and fighting, and frequently the master cock is kept so busy fighting intruders that he has little or no time for mating. In the confusion that results, I have seen a large group of hens singly or in small groups gradually drift away and join a smaller group of hens at a mating spot where mating was going on in an orderly way. By this system of establishing dominance, only the most vigorous and usually largest cocks ever attain the rank of master cocks. It is a curious fact that the same identical mating spot has been used for two, three, or in one case, four years. Whether this indicated that the same master cock is in charge, I do not know. It may be possible.

The behavior of hens is seldom aggressive. A hen ready to mate will sometimes peck another hen and drive her away from the master cock. One hen pecked at the master cock, apparently because he was mating with another hen. The hen signified readiness for mating by spreading or fluttering the wings, squatting down, and looking back toward the master cock. Occasionally a hen attempts to mount another hen that is ready for mating.

According to my observations, in all three species, the great majority of females are mated by only a small percentage of the dominant males. In the sage grouse, it was found that less than 3 per cent of the cocks mated with about 87 per cent of the hens. (For additional details, see "Auk," October, 1942.) In the other two species, the percentage of males successful in mating is possibly very small, but, due to the nature of the social organization, it is probably not so limited as in the sage grouse.

Work To Be Done. There were other interesting results. For example, sage grouse hens do considerable feeding while they are on the strutting area, but the cocks do little. Repeated infections with coccidia occur, and daily collections of feces showed that many more birds were infected with coccidia and that the infections were much heavier during full moon than at any time during the dark phases of the moon. As a result, the parasite is spread widely among the hens, which scatter it to the isolated spots where they nest and raise their young. So, the annual gathering serves as an important means to insure the continued life history of the coccidium.

It is certain that the sage grouse has more than 30 "words" or sounds and intonations that have a meaning they understand. One call by one bird, indicating the approach of an eagle, will cause every bird on the area to crouch low, alert to take wing when the eagle approaches nearer. A comparative study of the language of these grouse would be intriguing and would no doubt disclose "root words" of possible phylogenetic significance. We have noted the similarity between cooing and booming. Also, one sound of the sharptail resembles the crowing of the ring-necked pheasant. If each author in this monograph had been present, he would have observed things I did not see. Particularly needed was one skilled in interpreting comparative animal psychology, as well as an animal philologist, a sound recorder, and a stenographer. Dr. Fuller, no doubt, could improve over my technique by using strategically placed microphones connected with a wire sound recorder, automatically connected with the operating mechanism of the camera.

Summary. This elementary study in the sociobiology of three species of grouse has brought out many interesting results.

(1) The basic behavior (annual and daily assemblies, use of oesophagus,

fighting, bluffing, tendency to develop territorial dominance, *etc.*) shows many similarities and resemblances.

(2) Each species has developed certain characteristic behavior of its own.

(3) A diminishing population trend on the strutting area and its effect on social integration has been noted in the sage grouse. Notes have been taken on the effects of changing social hierarchies on individuals and on mating-spot groups, but these have not been analyzed.

(4) We have found cooperation related to specific communication systems, a very considerable degree of social interdependence, and what appear to be individual differences in the social role.

(5) The greater prairie chicken, the prairie sharptail grouse, and the sage grouse rank in this order in increasing complexity of social organization.

(6) The chief activities of all three species during the mating cycle center around rivalry for dominance among the males and competition of the males to attract or win the attention of the females.

References

1. Bailey, F. M. 1921. Handbook of Birds of the Western United States. Rev. ed: 134. Houghton-Mifflin. Boston.
2. Scott, J. W. 1942. Mating behavior of the sage grouse. Auk **59**: 477–498.
3. Simon, J. R. 1940. Mating performance of the sage grouse. Auk **57**: 467–471.

SOCIAL LIFE AND THE INDIVIDUAL AMONG VERTEBRATE ANIMALS

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The purpose of this brief review is to point out certain general problems in the study of vertebrate animal societies in relation to individuals and to illustrate and appraise the methods used in their solution. By determining those methods which have been used most successfully in previous experiments, we should gain some guidance for further investigations. The review and integration of facts already gained can in itself often be considered a stimulus to further progress.

Discussion of methodology in this field, as in others, may well proceed in conjunction with discussion of significant problems. The careful delineation of such problems depends on adequate field studies, since such studies set the stage for further analysis.

The reviews of Allee,[1,3] Friedmann,[38] Alverdes,[7,8] Wheeler,[93] and others indicate that aggregations are of frequent and very general occurrence in the animal kingdom. Random distribution of animals seems to be the exception rather than the rule with most animals. The organization of animal groups is based on both competitive and cooperative relations, and the wide individual differences which have been detected in each of these two aspects of social organization demand some means of measurement in the interests of more precise analysis and understanding. Competition and cooperation will each be considered separately in relation to individual differences.

Dominance Hierarchies as an Example of Competition

Intra- and interspecies dominance hierarchies based on aggressive-submissive interactions are of widespread occurrence among vertebrate animals both in the field and laboratory.[23] Although dominance hierarchies are not devoid of cooperative effects,[23,46] they reflect and will be taken as examples for analysis of one aspect of intragroup competition. Such analysis proceeds by means of preliminary description, identification, control and quantification of significant factors, and statistical evaluation of factors which cannot be readily controlled.

Progress in preliminary description of dominance hierarchies has depended strongly, although not necessarily, on the use of marked individuals. Dominance hierarchies have long been known to occur in flocks of chickens marked as individuals, where each individual except the one at the bottom of the hierarchy may peck or threaten certain other individuals without being pecked in return.[79,80,66] Each chicken also has precedence to food over its subordinates.

By watching wild ring-necked pheasants which had been trapped and,

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* Grateful acknowledgment is made to the American Psychological Association and to the publishers of the "Condor" for permission to reproduce previously published figures.

before release, marked with colored coroseal tags pinned to the skin at the back of the neck with a safety pin, we were recently able to demonstrate that dominance hierarchies occur among these birds during the winter.[25] This endeavor was in good part stimulated by previous studies in the domestic fowl, which also belongs to the pheasant family (*Phasianidae*), and illustrates that, on occasion, detailed descriptive studies of animals in pens or laboratories provide fruitful lines of inquiry for field studies.

The method of marking the birds was devised by Taber. By using a large colored number fastened on a coroseal tag of a still different color, a large number of individuals could be distinctively marked in a way that was readily visible with or without field glasses, depending on the distance from the blind. The ability to mark many individuals was a matter of importance, since many of the individuals marked were rarely seen after release.

The usual method of quantification in the study of dominance hierarchies has been to tabulate the relative frequency of threats or blows administered and received by each individual in relation to every other individual in a group. In the laboratory, this is done under standard systematically varied conditions in regular observation periods of given length. Precedence to food is often used as an index to dominance, particularly in studies with nonhuman primates. No single method gives a good measure of the degree of dominance, and use of a variety of suitable indices may help increase the reliability of the dominance order. Also, it is of practical importance in field studies, where it is often difficult to gather sufficient data from any single criterion to work out dominance relations with any degree of completeness.

Effects of Rank in the Dominance Hierarchy on the Individual. A general problem of much interest concerns the effects of the social hierarchy on the individual. The solution of this problem requires observation under field conditions as well as under varying degrees of experimental control. The social rank of an individual has profound effects on its existence. Individuals of low rank are frequently denied access to food and mates[23] and there is evidence that at times they may be prevented or delayed in the establishment of territories.[23,25,43]

The social hierarchy in a group of individuals that continue to live together is based on habitual subordination and makes for social harmony by stabilizing, ameliorating, and formalizing competitive relations.[46] Removal of the most dominant individuals reveals the previous suppression of individuals of lower rank, since increased aggressiveness is displayed by the remaining individuals, particularly those which had ranked just below the removed despot, as observed in chickens (unpubl.), cats,[95] rhesus monkeys,[19] and children.[63] Within the groups, displaced aggression, *i.e.*, passing on of punishment received from a despot to a subordinate, has been observed in a number of birds and mammals.[58,23] Another type of response to excessive domination is indicated by the observation that rats which are strongly dominated in their home cages are more likely to freeze into an unresponsive immobility during learning trials in a maze or puzzle box.[78]

Territorialism or the defense of given areas occurs among many vertebrate animals and may often intergrade with social organization based on dominance hierarchies.[23] In laboratory groups, each composed of four immature sunfish, Greenberg[43] observed that subordinates frequently defended areas against all but the most dominant fish. When three members of a group defended areas, the fourth was almost always driven about and severely punished. Its removal or death was followed by increased frequency of aggressive contacts among the territory holders. Introduction of a newcomer led to their attacking it instead of one another.

In general, among aggressive species of vertebrates, strangers are likely to be attacked and excluded from the group area or relegated to a low place in the dominance hierarchy.[23] In wild coveys of valley quail,[55] recently introduced birds were almost invariably found a few yards from the main body of natives and did not mingle until after a period of acquaintanceship. Alien quail in a covey actively dominated birds of subsequent introductions. Similarly, Guhl and Allee[46] found a significant positive correlation between seniority and social status in their flocks of hens with shifting membership. In small flocks of hens, it was recently observed that newcomers which managed to achieve high rank in the dominance hierarchy were permitted to join the group within a few days; newcomers of low rank required several weeks or more.[31] Some individuals were unable under certain conditions to become or to remain assimilated. Among free-ranging rhesus monkeys, young males which have matured sexually but which cannot maintain a low-order dominance rank may be driven out of the group by repeated attacks from dominant males and females, become negatively conditioned to the group as a whole, and avoid it. Two mature males with low dominance ranks may associate together and, by coordinating their behavior, maintain social status in the group against the resistance of other animals.[20]

Animals evicted from their territories or otherwise forced to wander in strange country may perhaps be assumed to be emotionally upset. For example, rats placed in a strange field have their feeding reactions more or less inhibited for some days thereafter and show increased urination and defecation. Quantitative study showed that individual differences in such reactions may be marked.[48]

Subordinate cocks of the domestic fowl are usually attacked by the dominant cock of a flock whenever they approach the hens, and after long continued persecution and suppression, they will tread much less frequently, even when tested in the absence of the dominant cock or with different hens. Guhl has dubbed this phenomenon "psychological castration."[47] The chronic effects of sex deprivation on animal behavior do not seem to have been much studied. Auto-erotic behavior has been reported for a number of birds and mammals, and among chimpanzees it is said usually to disappear when sexually mature individuals of both sexes have access to one another.[10] Carpenter,[19] however, has noted the phenomenon in an adult, free-ranging rhesus monkey which was at the top of its dominance hierarchy and which had ready access to females.

In evaluating the consequences of a low dominance position, the importance of carrying observations past one generation has recently been made evident by the work of Calhoun.[16] He observed that rats living in submarginal areas, with reference to a central food source, grew slowly, usually occupied a low social status, and rarely raised litters. In contrast, rats born in more favorable locations, with reference to the central food source, grew more rapidly and their greater weight usually enabled them to win higher rank in the dominance scale.

Basis for Rank in the Dominance Hierarchy. Another general problem of intragroup competition concerns not the consequences but the causes of a given social rank in the dominance hierarchy. There is a growing body of evidence that such social rank is generally decided by fighting, bluffing, or passive submission at the initial encounter between any given pair of individuals, or by an early series of such encounters.[22,23,43] When two well-acquainted hens are introduced into a strange flock, the dominant individual may facilitate rise of its subordinate partner in the social scale.[22,31] Douglis made the interesting observation that there was apparently no pecking by the dominant bird of its subordinate partner before both hens became assimilated into the new group.

Unfavorable emotional experiences may lead to chronic physiological changes which probably exert some influence on rank in the dominance hierarchy. Cats, subjected to an air blast when fed, develop a chronic fear state and are more likely to become engaged in fights with their subordinates.[65] Dogs, in an experimentally induced state of chronic anxiety, characterized by such things as hyperirritability and excessive autonomic reactivity, have been noted to be at or near the bottom of the dominance hierarchy in a group of dogs.[9,39] In the goat, Liddell and his associates[63a] have observed that, under certain experimental conditions, short pauses (2 minutes) between recurring signals for an impending electric shock on the foreleg gradually lead to a chronic state of tonic immobility, whereas longer pauses (6 minutes) result in chronic agitation. It would be of interest to work out on a sufficiently large scale the effects of each type of condition as produced by this method, as well as of therapeutic measures, on rank in the dominance hierarchy.

A considerable body of data exists to support various principles of learning, and application of such principles to experiments on social organization provides a number of working hypotheses. It is known that much previous success of a mouse during initial encounters with other mice increases its chances of winning subsequent bouts, whereas previous failures are very potent in facilitation of subsequent avoidance of other mice.[41] In the case of mice previously subjected to many defeats, it was found necessary to isolate them for a time before they could be trained to be more aggressive. When submissive mice are trained to be aggressive, Scott has observed that such external reactions as hair fluffing and tail rattling appear especially during a time of indecision, when the animal has stopped running away but has not yet begun to attack.[85]

Many factors influence the outcome of initial encounters and form an interacting complex, not all elements of which can be readily isolated and controlled, except by statistical means. An attempt in this direction was made with normal white leghorn hens from different flocks, with such important variables as sex, territorial familiarity, and social facilitation being controlled. Two hundred encounters, with two individuals for each encounter, were staged in a neutral pen, and the degree of association with success of the less easily controlled factors was measured by use of a modified biserial correlation formula. Evaluation of the contributions to success of these factors was made by use of Wright's path coefficient method, which, in this instance, was essentially the same as the multiple regression method. Factors of major importance were male hormone output, as indicated by comb size and slightness of moult. Degree of moult was considered to be a rough indicator of thyroid secretion, since moulting in chickens is apparently associated with seasonal hyperthyroidism. Social rank in the home flock and relative body weight had only minor influence. The multiple correlation coefficient of success with the four factors analyzed was 0.75. The degree of determination of the variance by the various factors was calculated to reduce the results to a percentage basis, and it was found that 56 per cent of the uncontrolled factors influencing success in this experiment were accounted for by differences in size of comb, moult, weight, and social rank in the home flock.[22]

Identification and abstraction of the essential features of a social situation permit one to devise relatively simple, schematic or formalized, and more precisely quantitative experiments, which lead to a clearer elucidation of basic principles and help uncover new factors. It is advisable to verify such experiments at each step in the analysis against the corresponding more complex social situation.

For example, the essential feature of aggressive food competition seems to be a conflict between fear of a despot and degree of hunger. One means by which fear can be quantified is by the degree of an administered electric shock, hunger by hours, or days of food deprivation, as illustrated in FIGURE 1. Rats subjected to varying degrees of starvation will readily cross a mildly charged, but not a strongly charged, electric grill for a food reward. An intermediate degree of electric shock gives intermediate results, *i.e.*, part of the rats are motivated mainly by hunger and part mainly by fear. In general, the frequency of crossings tends to increase with degree of hunger up to the point where physical exhaustion sets in with more severe degrees of starvation.[52]

Mild and moderate punishment may be illustrated by the pecking over food in a typical, organized flock of hens. In a regularly fed flock, hens of low rank in the dominance hierarchy frequently keep away from the food hopper until the more dominant hens have fed, or quickly retreat on mild threat. After one or two days without rations, it takes considerable pecking by the dominants to keep low ranking hens from the food; while after the flock of hens has been starved for a week, the low ranking hens will often continue to feed avidly in spite of all the pecks which their dominants rain upon them (unpubl.). Severe punishment may be illustrated by a flock of domestic cocks, particularly in the presence of hens. Some cocks may be so strongly suppressed that they spend most of their time on the roost, lose considerable weight, and venture to the floor to feed only when the dominant cock goes to the roost.[47]

Another formal method of measuring motivation was used with rats which pulled against a calibrated spring attached to a marker tracing on a polygraph so that the average force of their pull could be computed. Rats restrained in an alley near food pulled toward the food reliably harder than those restrained farther away. Rats given a brief electric shock at the same end of the alley pulled away harder when restrained near the place of shock than when restrained farther away. The avoidance gradient was steeper than the approach tendency, and, as a result, the rats approached close to the food-shock spot where avoidance and approach tendencies balanced and then stopped, showing some tendency to vacillate apparently because of their momentum.[69] This reminds one of the situation described by Howard and Emlen,[55] in which a strange valley quail attaches itself to and follows the nearest covey about for weeks, but generally at a little distance because of the likelihood of attack from covey members. Similarly, Zuckerman[99] has described how bachelor baboons may attach themselves to the harem of a mature male as closely as their fear of the despotic male allows.

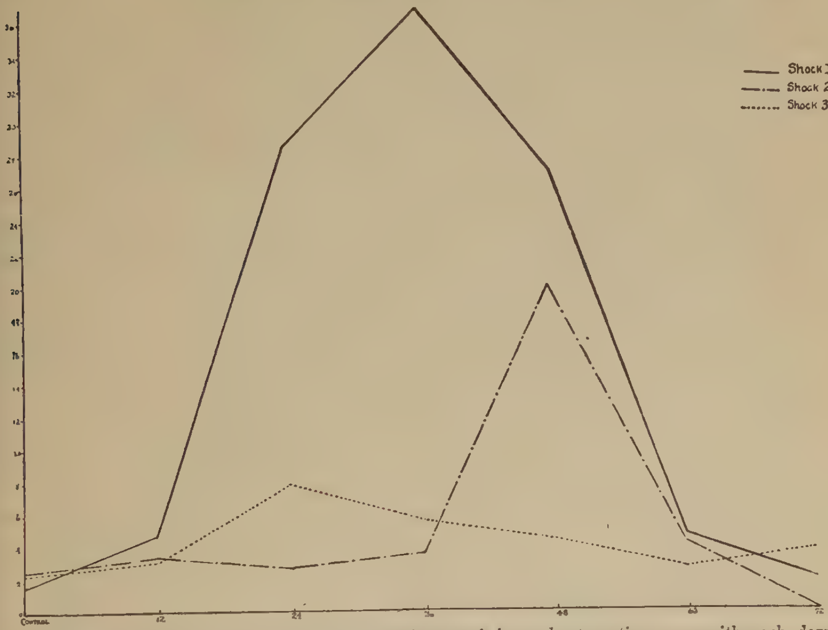

FIGURE 1. Showing the median number of crossings made by each starvation group with each degree of shock. Ordinates indicate the number of crossings, the abscissas, number of hours starvation.
(Comp. Psychol. Monogr. III (17): 152)

Determination of the physiological constants which are most significant for social behavior, together with study of their systematic variations, is an important means of integration of related behavior patterns, as illustrated by recent studies on sex hormones. This phase of the subject, as related to aggressive-submissive behavior, has been reviewed elsewhere.[23]

Cooperative Behavior

Aggressive dominance has been considered as an example of competitive behavior. As examples of cooperative behavior, *i.e.*, behavior which enhances group survival, attention will now be given to the effects of the group on individual welfare and survival, the mechanisms of group formation, and leadership.

Effects of the Group on Individual Welfare and Survival. During the early part of this century, many biologists seemed convinced that the effects of crowding on individual survival and reproduction were predominantly harmful. Allee,[1,3,4] however, has summarized many benefits of moderate crowding among animals often considered as being sub-social in nature, including such things as increased reproductive rate, favorable conditioning of the medium, and protection from such adverse environmental effects as heat, cold, toxic substances, and radical changes in osmotic pressure. The method of study included systematic variation in population density under adverse environmental conditions with subsequent precise measurement of the rate of reproduction, survival, or growth.

A few examples may be given, from animals kept under more or less artificial conditions, to illustrate the profound effects of social exclusion on individual welfare and survival. Unfortunately, observations under natural conditions seem to be scarce. Isolated Bobwhite quail are subject to greatly increased mortality from cold.[40] Isolated mice grow poorly and may develop skin eruptions on the head. These skin disorders seem to be largely prevented among grouped mice which lick the sores on the heads of each other (*cf.* Allee[2]). Rhesus monkeys, isolated so that they cannot groom each other, often develop heavy infestations of lice.[17] Young rhesus monkeys which are not cared for and protected by their mothers are likely to be killed by members of their own parent groups.[18]

Mechanisms of Group Formation. In view of its importance, it is not surprising that group formation can be stimulated by a variety of mechanisms. Correspondingly, a variety of methods is required for the elucidation of these mechanisms.

Specific attractions which may reflect specific physiological states comprise one class of mechanisms of group formation. This is well illustrated by formation of the sex pair. Breder[14] could elicit at will spawning or fighting reactions in male sunfish by moving an oval, grey cardboard shaped like a female or male, respectively. Successful attraction of the female and completion of fertilization among European three-spined sticklebacks involves a chain of stimuli and responses; each of the latter serves as the stimulus to the next step in the series. Methods of analysis of such specific communication systems have recently been summarized by Tinbergen.[92] He has emphasized use of models and the relative importance under certain conditions of successive tests in contrast to choice experiments, particularly on the grounds that the latent effects of stimulation by the more potent stimuli may be generalized to less effective stimulus objects. For example, male grayling butterflies with the scent glands removed were accepted just as frequently as normal males by the females when presented simultaneously, but they were much less successful when presented in turn. Under certain other conditions, the choice method has been employed with some success, and evidence of this type, for sexual selection of particular males by the female, has been reported for jewel fish,[73] chameleons,[42] and shell parakeets.[21] These experiments involved males with appearance artificially modified. Domestic hens may select particular males; Guhl[45] has discussed some of the complexities involved. The possible choice of particular females by the male is a matter that has received little critical attention.[47]

The observations of Selous on the ruff suggest the possibility that sexual selection may occur in some species in nature, since copulation in this case generally occurred on female invitation and after apparent selection of particular males (*cf.* Armstrong: 218–223[10]). However, each male also stays in a definite spot or territory in the group arena.

The choice method was used by Blair and Howard[15] on deer-mice of different subspecies and color varieties. In each of their experiments, four mice were placed in four mouse cages interconnected by short tunnels, and the tendency to aggregate in one box or to stay in different boxes was checked daily until litters appeared. There was a significant tendency for mice of dark or pale strains of *Peromyscus maniculatus blandus* to mate with their own color type.

The schooling of fish provides other examples of specific attractions favoring group formation.[14] *Brachydanio rerio* approaches moving targets of any shape up to a certain size; from shapes beyond that size, they retreat. However, any such stimulus soon loses its potency. Fish vary greatly in their tendency to form a school, and this suggests the desirability of quantitative measures of degree of aggregating tendency. Some such measures have been discussed by Breder and Halpern.[14]

Specific tolerances are very important factors in group formation.[23] Such factors vary with the species, sex, parental motivation, external danger, hunger, and degree of acquaintanceship. An example may be given from studies made at the New York Zoological Park in the summer of 1947. A group of white-tailed deer in a large enclosure, consisting of 6 does and 2 bucks, was found to have a dominance order with well-marked and consistent aggressive-submissive interactions in food competition. These deer were frequently scattered widely over the enclosure. On the other hand, a group of 5 female Nyala antelope, with no apparent aggressive interactions, moved about usually as a compact herd unit in another large enclosure (the "African Plains"). A mature buck associated with these females, and generally kept a younger, immature buck at some little distance from them.

Group formation in many species evidently depends on a balance between individual aggressiveness and more social tendencies. Winter flocks of birds often break up and scatter out to individual breeding territories in early spring, particularly during warm weather and coincident with the increased intragroup aggression that accompanies onset of the breeding season.[75] In very small cages, violent fighting is likely to develop between the male and female of a pair of pigeons resulting in injury to the female, eggs, and young.[53] The attachment of female rhesus monkeys to their young under normal conditions may be extremely intense, but, under conditions of malnutrition and close confinement, females often lose much of their maternal drive, fight their infants away from food, and may even kill them.[17]

Emotional experiences of individual animals may have a marked influence on their gregariousness. Shyness is one of the striking symptoms of dogs and sheep in which a state of chronic anxiety has been experimentally induced.[9] Such dogs do not join in the playful running and barking of other dogs, and these sheep, while feeding in the pasture, are often well apart from the main body of the flock. One such sheep left the group when dogs attacked the flock and, thus, was singled out and killed.

The members of a social group may become conditioned to one another, and the repetition of social experiences which apparently provide mutual satisfactions may function strongly to maintain the group. Food-sharing behavior occurs much more frequently between young chimpanzees which previously had established a close friendship than among those not intimate with each other.[76] In a colony of 14 black-footed and Humboldt penguins and their hybrids, which were watched for one summer at the New York Zoological Park, mutual preening was very frequently observed within a sex pair but was never seen to occur between members of different sex pairs (in press). Skutch[87] has suggested that, in the most highly social birds, individuals other than mates may preen each other. The marbled wood-quail which he observed in Costa Rica traveled in coveys of eight individuals or fewer, preened each other's plumage, and were not seen to fight or peck over food. A nesting pair of black-crowned night herons practices a greeting ceremony in which the long nuptial plumes of the crown are erected. Removal of these plumes tends to disintegrate the pair and the birds stand apart or seek new mates.[74]

A highly important basis for group formation and maintenance is related to socialization of the young. Many young vertebrate animals seem to be highly social or to aggregate closely compared with the adults, for example: most fishes,[14] mallard ducklings (as can readily be observed in many of our public parks), and young chimpanzees.[97] Both innate and learned factors are involved. Noble and Curtis[73] have evidence that species of fish which develop red breeding colors are attracted more by red early in life and those that develop black breeding colors are attracted more by black early in life. They state that association with the parents tends to strengthen the inherited tendency to swim toward moving disks of a particular color, since young reared in isolation are slow to respond.

Very early experience may be of considerable importance in determining the later associates of social animals. Doves and pigeons reared by another species, may, after they reach sexual maturity, associate with the species that reared them in preference to their own.[26,94] Young doves which have never mated are more likely to enter into homosexual matings than birds which have been normally paired with the opposite sex, according to Craig.[27] Craig[28] observed that male ring doves raised in isolation from other doves attach their social reactions to humans but can gradually transfer them to doves later on. In the guinea pig, there is some evidence of reluctance of a male to mate with females of the same litter as himself.[64]

In an attempt to measure social appetite of chicks, Murchison[72] devised a piece of apparatus known as a "social runway." This consists of a long runway with cheese cloth walls, brightly illuminated within and having at either end a box in which a chick can be placed behind a pane of glass. The glass is lifted simultaneously at either end of the runway and the chicks generally walk or run toward each other until they meet. Recently, Miss Margaret Pollock and the author (unpubl.) used a modified version of this apparatus and observed that 10 chicks which had been isolated in small cages for 11 or more days after hatching covered less than one-fourth the distance run by the 10 controls against which they were matched. The controls uniformly peeped after the fashion of a lost chick just before the run began, and each isolate uniformly pecked at the control upon meeting it in the runway.* After two months, the surviving chicks were turned loose in a courtyard about 20 feet wide × 30 feet long, and, by recording at 5-minute intervals the number of times each chick was more than 4 feet from its nearest neighbor, it was soon found that the chicks that had been isolated early in life had a somewhat greater tendency to keep apart from the group. Scott[84] has observed that a female lamb, raised on a bottle and permitted no contact with other sheep until 10 days after birth, was rebuffed by the other sheep and thereafter tended to keep apart from the group, for as long as 3 years.

Mead[67] has remarked on the association of aggressiveness with the rough and abbreviated nursing habits of one primitive tribe in contrast to the gentle and prolonged nursing of infants in a more cooperative primitive tribe. This gave us a working hypothesis, and, using a modified Hall-Klein[49] scale, Douglas Heath[51] found a significantly greater degree of aggressiveness in 9 early weaned rats, as compared to 9 young rats permitted to remain with their mothers.† The rats were tested at about two months of age by means of paired encounters between early and late weaned rats. There was little correlation between weight and aggressiveness. It would be desirable to repeat this study on a larger scale and to equate the degree of handling of control and experimental rats.

Aggressiveness often seems to grow out of play fighting in young animals, but play itself may help condition the young to cooperative, group-positive behavior.[18] This and other concepts of play in animals have been recently reviewed by Beach.[12]

Another mechanism of group formation or maintenance requiring entirely different techniques for its study is that of traditional locality fixation. With the cooperation of various state agencies, Emlen found that the location of some of the winter crow roosts in New York State[34] and in California[36] had not changed appreciably for as long as 50 years, despite radical changes in existing vegetation cover and other factors. It is said that prairie sharp-tailed grouse have been known to frequent the same dancing and display arena beyond the tribal memory of local Indians.[10] Bass Rock, a small island in the Firth of Forth, Scotland, is a famous breeding site for gannets, and these birds are known to have occurred on this island up to at least 500 years ago.[47a] A colony of European blue herons is known to have existed on the castle park grounds at Chilham in Kent, England, since the 13th century.[75a]

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* Recently, I found that newly hatched chicks will not readily approach each other, even when only a few inches apart, until after they have had a few minutes actual contact with each other (unpubl.).

† This study was done under the supervision of the author at Amherst College, Mass.

Leadership and Contagious Behavior. The social role of particular individuals in enhancing group cooperation may vary greatly. As an example, the phenomenon of leadership will be considered. By leadership is meant any activity of an individual or small group of individuals which initiates or stimulates similar activity by other individuals. As ordinarily used, it implies that leadership by a given individual is more or less consistent, and it does not imply coercion. However, the line is sometimes difficult to draw. Such leadership has been reported in a number of vertebrates. A statistical type of leadership has been shown by tabulating frequency of definite incidents of leadership. Among White Pekin ducks, some individuals may lead definite flock movements much more frequently than do other individuals, although leadership shifts a good deal from one individual to another.[6]

Leadership may have various functions. Among rhesus monkeys, the supreme despot may aid the group to maintain a much larger territory than it could do in his absence.[17,18] The same is probably true of blue geese.[57] Leadership may furnish guidance to group movements. Goldfish[3] learn to run a simple maze to a food reward more quickly in company with experienced individuals. Rats soon learn that the direction taken by an experienced leader means a food reward. Thirst and water can readily be substituted for hunger and food and the leader will still be followed.[70] Quail and grouse in the wild probably learn to eat new foods from experienced individuals.[61] Dove[32] observed that 40 chicks of the domestic fowl which were fed a mixture of foods as selected by the fastest growing individuals grew to a weight one-fourth greater than the average of an equal number of chicks fed on a mixture selected by the slowest growing chicks. He suggested that the ability of the leader to select a suitable diet might influence the survival or nonsurvival of a group of animals. The leader may often act as sentinel, as in blue geese[57] and red deer.[30] Training of the young by the parents in the group is a phase of leadership in a sense. It is particularly important among higher primates, such as chimpanzees,[97] but the matter seems to have been much less studied among lower vertebrates.

Of particular significance in connection with the origin of leadership is the phenomenon of contagious behavior, in which activity of any individual stimulates similar activity on the part of another. Response of the latter may in turn act back on the first animal. The reaction is circular and, as a result, is intensified and may also spread throughout the group. A flock of various species of geese which the author observed for one summer at the New York Zoological Park showed a strong tendency to feed, swim, bathe, preen, and rest as a group. Armstrong[10] has reviewed many similar examples in birds. Movement of individual fish may stimulate and direct similar movement among other fish.[14] Platt and Dare[77] observed that young homing pigeons found their way home much sooner as a group than when flown as individuals. The example of another feeding individual stimulates hens to eat more.[11] Nestlings of the starling may stimulate each other to gape for food.[54] Fear is contagious, as seen in a flock of sheep or herd of cattle. Predation is contagious, as seen in the killing of mice and rats by cats.[60] The development of crowing in young cockerels is hastened if they can hear the adult cocks crowing.[58] Singing stimulates singing in house wrens[59] and in song sparrows.[75] Pairing by some individuals stimulates pairing in other members of a covey of valley quail.[37]

The factors that make for leadership need further elucidation and investigation. In some species, the leader of the group movements is also the despot. Sunfish show a definite tendency for leadership through a door to a food reward to be correlated with despotism.[43] Among moving stallions, the despot is likely to attack any stallion that forges ahead of him (Brayton Eddy, personal communication). Among goats, however, there is some evidence that the despot is not necessarily the leader.[88] Leadership may often depend on experience. Craig[26] states that among breeding ring doves, if only one bird of a pair is experienced, this bird takes the lead in most of the operations. Among sheep, the oldest ewe is generally the leader.[84]

Leadership implies followership and the latter may depend partly on learning the benefits of social life and partly on innate followership tendencies. In many avian species, it seems evident that to a young bird the parent represents a food reward as well as warmth, and it is not long before the young bird begins to follow the parent about begging for food. According to Dove,[32] the young of horses, cattle, swine, goats, rabbits, and chickens learn very early to follow the mother and to feed at the same time and on the same foods as does the mother. Young kittens will kill mice or rats after seeing their mother do so and are particularly prone to attack the same kind of rat or mouse as does the mother.[60] Parent pheasants[90] are particularly alert and it is not improbable that the young learn by association with the mother's alarm behavior to distinguish some of their enemies (*cf.* Nice: 66[75]).

Physiology and Genetics. Some of the significant physiological constants for such cooperative activities as sexual and parental behavior have been reviewed elsewhere[13,24] and provide many striking examples of the importance of physiological sociology in integrating diverse behavioral phenomena. For example, injection of a pituitary hormone, prolactin, may induce the whole pattern of incubation and parental behavior in domestic hens, particularly in hens that have been in active egg production (*ibid*).

Some progress has been made in the analysis of the genetics of parental behavior in domestic fowl.[44,50] Degree of broodiness is measured by annual number of broody periods, since the length of individual broody periods (when promptly discouraged to restore egg production) remains rather constant in flocks bred to reduce broodiness. The evidence indicates that the inheritance of broodiness depends on two complementary dominant genes. The existence of other genes for broodiness is indicated by the failure of 18 years' selective breeding in a flock of Rhode Island Reds to free it entirely from broodiness. A little progress is being made on the physiological genetics of broodiness. Thus, fowl of "nonbroody" breeds contain less pituitary prolactin and are less responsive to prolactin injections than are fowl of broody races.[24]

Social Groups and Population Density

In order to attain a complete appreciation of the relationship of social organization to the economy of a species it is necessary to consider the reciprocal effects of social phenomena and population density.[23] The emphasis here on social factors does not of course imply that other factors fail to exert important regulatory effects on population density.

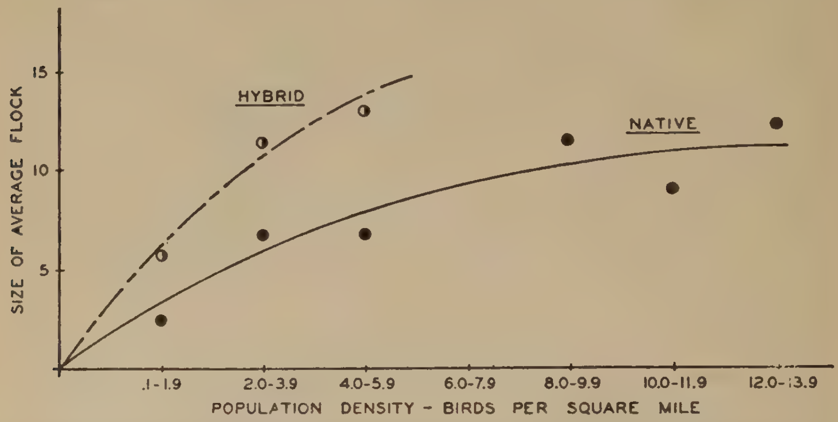

FIGURE 2. Relation of flock size to population density in native and hybrid turkey popu lations; based on 58 native and 37 hybrid flocks tallied in the winter censuses of the study areas over the per iod 1940 to 1943. (Condor, 46: 152)

Population units tend to maintain a rough balance with the habitat, and the existence of harmful effects from too low, as well as from too high, a population density seems probable for many species on the basis of both field and laboratory studies.[1,3,4,5]

The average size of flocks of wild turkeys gradually increases with population density, as may be seen from FIGURE 2, which is taken from Leopold's[62] study in Missouri. This means that the number and complexity of social relations will be greatly multiplied and raises the problem as to the number of individuals that can be added to a closely organized group without breaking down its organization.

One mode of organization concerns the dominance hierarchy. There is some evidence that such hierarchies occur in wild turkeys.[71] It seems doubtful that the ability to maintain a dominance hierarchy would be seriously affected by an increase in average flock size from 5 to 10 birds. It seems not unlikely, however, that there would be some increase in tension within the group, and there may be other important but as yet unknown effects on survival and reproduction. Guhl (personal communication) observed that, in a flock of 97 domestic hens, the birds were able to maintain a dominance hierarchy (the dominance relations in 94 per cent of the possible pairings were observed), although shifts in dominance rank were relatively frequent compared with small flocks.

Recency of the flock organization may be a more important factor than mere size. At high population densities, there may be more reshuffling of group membership. In stable, well-organized flocks of hens, as compared with groups kept in a state of social disorganization by a shifting membership, the average individual gets more to eat, maintains body weight better, and probably lays more eggs.[46] At low population densities, social barriers among valley quail are more rigidly enforced, and strange individuals are more likely to be forcibly excluded.[35,55] This would permit the covey to maintain the same restricted individual composition for a longer period of time.

Social Life and Evolution

Application of the general principles of evolution to social life gives a method of evaluating the forces that have shaped animal societies. Such principles can also be used to help clarify social behavior patterns that have become abbreviated and ritualized in the course of evolution.[91] Of particular interest is the relationship between competition and cooperation. Allee[4,5] has pointed out that the very existence and general occurrence of metazoan animals and of complex animal societies is evidence that, in the long run, cooperation has been more effective than individual competition. There has been a general trend toward increasing complexity and increasing environmental control by living organisms. Cooperation is more characteristic and has been carried to a further degree in the individual organism and in the intraspecies population than in the interspecies community, but it has evolved in all systems.[33]

In the higher animals, there is relatively more emphasis on the individual, as well as on the group, compared to lower animals.[86] Vertebrate societies seem to be characterized by a greater individual plasticity and a greater emphasis on general individual competition than are the more complex insect societies. Classification of vertebrate social groups according to the degree of integration reveals, however, that increase in cooperative aggression by the group as the competing unit is paralleled by decrease in intragroup aggression.[23] In both insect and vertebrate societies, maintenance of cooperative relations depends to a large extent on socialization of the young.[81,82] Among vertebrates, this trend reaches its climax in the primates.[98]

Another type of question concerns the best conditions for the evolution of social life. Selection within the species between many small and partially isolated populations not too rigidly limited by selection provides the most favorable conditions for establishment of socially advantageous but individually disadvantageous genetic variations.[96] Sturtevant[89] has suggested that such a population breeding structure helps account for the establishment of sterile castes among the social insects. Among vertebrates, parental care represents a somewhat different case from the above. Such care may at times be individually disadvantageous to the parents; but it is particularly favored by evolution, because such traits are directly enhanced by the better chances of survival of the progeny.* That the population breeding structure postulated by Wright finds some counterpart in nature has been shown for certain species of birds by Miller.[68]

To some extent, studies of animal societies may find human applications. Since man is an animal, it may be possible by the study of animal societies to discover significant relationships between diverse phenomena which indicate universal principles applicable to both.[33] This is quite obvious in the case of physiological sociology but less so in the case of ecological sociology. Studies of abnormal behavior in animals may help throw some light on certain not entirely dissimilar phenomena in man.

Social nongenic inheritance has given man a tremendous advantage over the lower animals, but it has at times produced increased stress on, or rendered maladaptive, man's biological nature. Selection for an immature type has made possible the prolonged education necessary to share in man's cultural progress but perhaps has also increased the likelihood of emotional disorders. Man's intelligence has produced a body of scientific and technical knowledge at an ever-increasing rate, showing none of the tendency toward self-limitation characteristic of other biological phenomena[56] (at least, not until man, under the most favorable conditions for large scale scientific research in history, managed to release atomic energy on a large scale). Biological phenomena are organized into a general competitive-cooperative pattern, but the biosphere viewed as a whole can be regarded as a basically cooperative venture in the transformation and control of other energy sources. The same now appears to be true of mankind, particularly in view of the possibilities of human global organization. To the extent that we can reason by analogy with lower levels of organization and from past biological experience, the basic tendency toward increased cooperativeness in the sense of mutually beneficial activities seems to be worth considering.

Conclusions

In the opinion of the author, those methods which have furthest advanced our understanding of animal societies in the recent past have been the more precise, quantitative, and continued programs which have focussed on individual differences in behavior at critical times and paid little attention to traditional interdisciplinary boundaries. Good field studies of animal societies necessarily provide the basic orientation for laboratory analysis. Unfortunately, they have often proved difficult and are therefore scarce. Field conditions of social organization may be very complex, and laboratory analysis makes it possible to analyze and, to some extent, to control the components of this complex. At the same time, laboratory studies may also suggest working hypotheses for further field studies and so exert a reciprocal influence on the latter. Experimental analysis, whether in the field or laboratory, should proceed in the light of a growing and self-consistent framework of pre-existing facts, each new fact providing a new opportunity to recheck this framework.

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* Personal communication from Dr. James Crow.

The synthesis of sex hormones and their ready availability to investigators of behavior have given impressive demonstrations of the value of a new tool, which owes its inception to advances in other fields of study.

The evolutionary viewpoint helps place man in his proper perspective in relation to other animals, and the steady accumulation of facts on human similarities and differences from nonhuman animals helps to make available an ever clearer picture.

Bibliography

1. Allee, W. C. 1931. Animal Aggregations: A Study in General Sociology. University of Chicago Press. Chicago.
2. Allee, W. C. 1935. Relatively simple animal aggregations. Handbook of Social Psychology, Edited by C. Murchison.: 919–946. Clark Univ. Press. Worcester, Mass.
3. Allee, W. C. 1938. The Social Life of Animals. W. W. Norton. New York.
4. Allee, W. C. 1943. Where angels fear to tread: a contribution from general sociology to human ethics. Science **97:** 517–25.
5. Allee, W. C. 1945. Human conflict and cooperation: the biological background. Approaches to National Unity (20): 321–67. Fifth Symposium of the Conference on Science, Philosophy, and Religion. Edited by L. Bryson, L. Finkelstein, and R. M. MacIver. Harper. New York.
6. Allee, W. C., M. N. Allee, F. Ritchey, & E. W. Castle. 1947. Leadership in a flock of White Pekin ducks. Ecology **28:** 310–15.
7. Alverdes, F. 1927. Social Life in the Animal World. Harcourt Brace. New York.
8. Alverdes, F. 1935. The behavior of mammalian herds and packs. Handbook of Social Psychology, Edited by C. Murchison. Clark Univ. Press. Worcester, Mass.
9. Anderson, O. D. & R. Parmenter. 1941. A long-term study of the experimental neurosis in the sheep and dog. Psychosomatic Med. Monog. **2:** 1–150.
10. Armstrong, W. A. 1947. Bird Display and Behaviour. Lindsay Drummond. London.
11. Bayer, E. 1929. Beiträge zur Zweikomponententheorie des Hungers. Zeitschrift für Psychologie **112:** 1–54.
12. Beach, F. A. 1945. Current concepts of play in animals. Amer. Nat. **79:** 523–41.
13. Beach, F. A. 1948. Hormones and Behavior. Paul B. Hoeber. New York.
14. Breder, C. M., Jr. & F. Halpern. 1946. Innate and acquired behavior affecting the aggregation of fishes. Physiol. Zool. **19:** 154–190.
15. Blair, W. F. & W. E. Howard. 1944. Experimental evidence of sexual isolation between three forms of mice of the cenospecies *Peromyscus maniculatus*. Contrib. Lab. Vert. Biol. Univ. Mich. No. 26.
16. Calhoun, J. B. 1948. The development and role of social status among wild Norway rats. Anat. Rec. (Suppl) **101:** 44.
17. Carpenter, C. R. 1942. Societies of monkeys and apes. Biological Symposia **7:** 177–204.
18. Carpenter, C. R. 1942. Characteristics of social behavior in non-human primates. Trans. N. Y. Acad. Sci., Ser. II, **4:** 248–58.
19. Carpenter, C. R. 1942. Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). II. Periodicity of estrus, homosexual, autoerotic and non-conformist behavior. Jour. Comp. Psychol. **33:** 113–42.
20. Carpenter, C. R. 1945. Concepts and problems of primate sociometry. Sociometry **8:** 56–61.

21. Cinat-Tomson, H. 1926. Die Geschlechtliche Zuchtwahl beim Wellensittich (*Melopsittacus undulatus Shin.*) Biolog. Zentralblatt **46:** 543–552.
22. Collias, N. E. 1943. Statistical analysis of factors which make for success in initial encounters between hens. American Naturalist **77:** 519–38.
23. Collias, N. E. 1944. Aggressive behavior among vertebrate animals. Physiological Zoology **17:** 83–123.
24. Collias, N. E. 1950. Steroid hormones and behavior with special reference to birds and to the mechanisms of hormone action. Symposium on Steroid Hormones. Edited by E. Gordon. Univ. of Wisconsin Press. Madison. In press.
25. Collias, N. E. & R. D. Taber. 1948. Grouping and dominance relations among wild ring-necked pheasants. Anat. Record (Suppl) **101:** 44–5.
26. Craig, W. 1908. The voices of pigeons regarded as a means of social control. Am. J. Soc. **14:** 86–100.
27. Craig, W. 1913. The stimulation and inhibition of ovulation in birds. J. Anim. Behav. **3:** 215–221.
28. Craig, W. 1914. Male doves reared in isolation. J. Anim. Behav. **4:** 121–133.
29. Crew, F. A. E. & L. Mirskaia. 1931. The effects of density on an adult mouse population. Biol. Generalis **7:** 239–50.
30. Darling, F. F. 1937. A Herd of Red Deer. Oxford Univ. Press. London.
31. Douglis, M. D. 1948. Social factors influencing the hierarchies of small flocks of the domestic hen: interactions between resident and part-time members of organized flocks. Physiological Zoology **21:** 147–182.
32. Dove, W. F. 1935. A study of individuality in the nutritive instincts and of the causes and effects of variations in the selection of foods. Amer. Nat. **69:** 469–44.
33. Emerson, A. E. 1946. The biological basis of social cooperation. I 11. Acad. Sciences Trans. **39:** 8–18.
34. Emlen, J. T. Jr. 1938. Midwinter distribution of the American crow in New York State. Ecology **19:** 264–75.
35. Emlen, J. T. Jr. 1939. Seasonal movements of a low-density valley quail population. J. Wildlife Management **3:** 118–30.
36. Emlen, J. T. Jr. 1940. The midwinter distribution of the crow in California. Condor **42:** 287–94.
37. Emlen, J. T. Jr. & F. W. Lorenz. 1942. Pairing responses of free-living valley quail to sex-hormone implants. Auk **59:** 369–78.
38. Friedmann, H. 1935. Bird societies. Handbook of Social Psychology, Edited by C. Murchison: 142–185. Clark Univ. Press. Worcester, Mass.
39. Gantt, W. H. 1944. Experimental Basis for Neurotic Behavior. Hoeber. New York.
40. Gerstell, R. 1939. Certain mechanisms of winter quail losses revealed by laboratory experimentation. Trans. Fourth N. A. Wildlife Conf., Washington: 462–68.
41. Ginsburg, B. & W. C. Allee. 1942. Some effects of conditioning on social dominance and subordination in inbred strains of mice. Physiol. Zool. **15:** 485–506.
42. Greenberg, B. & G. K. Noble. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Vogt). Physiol. Zool. **17:** 392–439.
43. Greenberg, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool. **20:** 267–299.
44. Goodale, H. D., R. Sanborn, & D. White. 1920. Broodiness in domestic fowl. Mass. Agri. Exp. Sta. Bull. **199:** 93–116.
45. Guhl, A. M. 1942. Social discrimination in small flocks of the common domestic fowl. J. Comp. Psychol. **34:** 127–48.
46. Guhl, A. M. & W. C. Allee. 1944. Some measurable effects of social organization in flocks of hens. Physiol. Zool. **17:** 320–47.
47. Guhl, A. M., N. E. Collias, & W. C. Allee. 1945. Mating behavior and the social hierarchy in small flocks of White Leghorns. Physiol. Zool. **18:** 365–90.
47a. Gurney, J. H. 1913. The Gannet. Witherby and Co. London.
48. Hall, C. S. 1934. Emotional behavior in the rat. I. Defecation and urination as measures of individual differences in emotionality. J. Comp. Psychol. **18:** 385–403.
49. Hall, C. S. & S. J. Klein. 1942. Individual differences in aggressiveness in rats. J. Comp. Psychol. **33:** 371–84.
50. Hays, F. A. 1940. Inheritance of broodiness in Rhode Island Reds. Mass. Agri. Exp. Sta. Bull. **377:** 1–11.
51. Heath, D. H. 1947. An experiment on early weaning and aggressiveness in rats. Unpublished.
52. Holden, F. 1926. A study of the effect of starvation upon behavior by means of the obstruction method. Comp. Psychol. Monog. **3** (17): 1–45.

53. Hollander, W. F. 1945. A type of psychopathy in the domestic pigeon. J. Comp. Psychol. **38:** 287–89.

54. Holzapfel, M. 1939. Analyse des Sperrens und Pickens in der Entwicklung des Stars. J. f. Ornith **87:** 525–553.

55. Howard, W. E. & J. T. Emlen, Jr. 1942. Intercovey, social relationships in the valley quail. Wilson Bull. **54:** 162–70.

56. Hutchinson, G. E. 1948. Circular causal systems in ecology. Ann. N. Y. Acad. Sci. **50**(4)**:** 221–46.

57. Jenkins, D. 1944. Territory as a result of despotism and social organization as shown by geese. Auk **61:** 30–47.

58. Katz, D. 1937. Animals and Men. Studies in comparative psychology. Longmans, Green. New York.

59. Kendeigh, S. C. 1941. Territorial and mating behavior of the house wren. Ill. Biol. Monog. **18** (3): 1–120.

60. Kuo, Z. T. 1931. The genesis of the cat's responses to the rat. J. Comp. Psychol. **11:** 1–35.

61. Leopold, A. 1933. Game Management. Scribners. New York.

62. Leopold, A. S. 1944. The nature of heritable wildness in turkeys. Condor **46:** 133–97.

63. Lewin, K., R. Lippitt, & R. K. White. 1939. Patterns of aggressive behavior in experimentaly created "social climates." J. soc. Psychol. **10:** 271–299.

63a. Liddell, H. S. 1947. The experimental neurosis. Ann. Rev. Physiol. **9:** 569–80.

64. Louttit, C. M. 1929. Reproductive behavior of the guinea pig. II. The ontogenesis of the reproductive behavior pattern. J. Comp. Psychol. **9:** 293–304.

65. Masserman, J. H. & P. Siever. 1944. Dominance, neurosis and aggression. Psychosomatic Med. **6:** 7–16.

66. Masure, R. & W. C. Allee. 1934. The social order in flocks of the common chicken and the pigeon. Auk **51:** 306–27.

67. Mead, M. 1935. Sex and temperament in three primitive societies. W. Morrow. New York.

68. Miller, A. H. 1947. Panmixia and population size with reference to birds. Evolution **1:** 186–90.

69. Miller, N. E. 1944. Experimental studies of conflict. Personality and the Behavior Disorders, edited by J. M. Hunt **I** (14): 431–67. Ronald Press. New York.

70. Miller, N. E. & J. Dollard. 1941. Social learning and imitation. Yale Univ. Press. New Haven.

71. Mosby, H. S. & C. O. Handley. 1943. The wild turkey in Virginia. Pittman-Robertson Projects—Division of Game. Richmond.

72. Murchison, C. 1935. The experimental measurement of a social hierarchy in *Gallus domesticus.* I. The direct identification and direct measurement of social reflex No. 1 and social reflex No. 2. J. Gen. Psychol. **12:** 3–39.

73. Noble, G. K. & B. Curtis. 1939. The social behavior of the jewel fish, *Hemichromis bimaculatus.* Bull. Amer. Mus. Nat. Hist. **76:** 1–76.

74. Noble, G. K. & M. Wurm. 1942. Further analysis of the social behavior of the Black-crowned Night Heron. Auk **59:** 205–24.

75. Nice, M. M. 1943. Studies in the life history of the song sparrow. II. The behavior of the song sparrow and other passerines. Trans. Linn. Soc. N. Y. **6:** 1–329.

75a. Nicholson, E. M. 1929. Report on the "British Birds" census of heronries, 1928. British Birds **22:** 333–72.

76. Nissen, H. W. & M. P. Crawford. 1936. A preliminary study of foodsharing behavior in young chimpanzees. J. Comp. Psychol. **22:** 383–419.

77. Platt, C. S. & R. S. Dare. 1945. The homing instinct in pigeons. Science **101:** 439–40.

78. Riess, B. F. 1946. "Freezing" behavior in rats and its social causation. J. Soc. Psychol. **24:** 249–51.

79. Schjelderup-Ebbe, T. 1922. Beiträge zur Sozialpsychologie des Haushuhns. Zeits. f. Psychol. **88:** 225–52.

80. Schjelderup-Ebbe, T. 1935. Social behavior of birds. Handbook of Social Psychology, Edited by C. Murchison (XX): 947–73. Clark Univ. Press. Worcester, Mass.

81. Schneirla, T. C. 1941. Social organization in insects, as related to individual function. Psychol. Rev. **48:** 465–86.

82. Schneirla, T. C. 1946. Problems in the biopsychology of social organization. J. Abnorm. & Soc. Psychol. **41:** 385–402.

83. Scott, J. P. 1945. Group formation determined by social behavior; a comparative study of two mammalian societies. Sociometry **8:** 42–52.
84. Scott, J. P. 1945. Social behavior, organization and leadership in a small flock of domestic sheep. Comp. Psychol. Monog. **18** (96): 1–29.
85. Scott, J. P. 1947. "Emotional" behavior of fighting mice caused by conflict between weak stimulatory and weak inhibitory training. J. Comp. & Physiol. Psychol. **40:** 275-82.
86. Simpson, G. 1941. The role of the individual in evolution. J. Wash. Acad. Sci. **31:** 1–20.
87. Skutch, A. F. 1947. Life history of the marbled wood-quail. Condor **49:** 217–32.
88. Stewart, J. C. & J. P. Scott. 1943. Lack of correlation between leadership and dominance relationships in a herd of goats. J. Comp. & Physiol. Psychol. **40:** 255–64.
89. Sturtevant, A. H. 1938. Essays on evolution. II. On the effect of selection on social insects. Quart. Rev. Biol. **13:** 74–76.
90. Taber, R. D. 1949. Observations on the breeding behavior of the ring-necked pheasant. Condor **51:** 153–175.
91. Tinbergen, N. 1939. On the analysis of social organization among vertebrates, with special reference to birds. Amer. Midl. Nat. **21:** 210–34.
92. Tinbergen, N. 1948. Social releasers and the experimental method required for their study. Wilson Bull. **60:** 6–51.
93. Wheeler, W. M. 1923. Social Life among the Insects. Harcourt Brace. New York.
94. Whitman, C. O. & H. Carr. 1919. The behavior of pigeons. Carnegie Inst. Publ. **257:** 1-161.
95. Winslow, C. N. 1938. Observations on dominance—subordination in cats J. Genet. Psychol. **52:** 425–28.
96. Wright, S. 1945. Tempo and mode in evolution: a critical review. Ecology **26:** 415–19.
97. Yerkes, R. M. 1943. Chimpanzees, a Laboratory Colony. Yale Univ. Press. New Haven.
98. Yerkes, R. M. & A. W. Yerkes. 1929. The Great Apes: A Study of Anthropoid Life. Yale Univ. Press. New Haven.
99. Zuckerman, S. 1932. The Social Life of Monkeys and Apes. Kegan, Paul, Trench, Trubner & Co. London.

THE ISOLATION OF FACTORS OF LEARNING AND NATIVE BEHAVIOR IN FIELD AND LABORATORY STUDIES*

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In his important recent paper on comparative behavior research, Lorenz[8] starts with the remark that "all living systems are, in their psychological structure, historical systems, and the understanding of all their characteristics is fundamentally impossible without insight into the historical development of the individual behavior pattern." This statement, translated into research terms and applied to laboratory and field studies, implies that longitudinal behavior research must cope with the problem of the origin of any given behavioral sequence. Those of us who, under the influence of the psychological teaching of the 1920's, believed that the so-called "instinct" controversy was dead, must of necessity revise our necropsies.

The impulse for this revision stems mainly from the results of carefully conducted field studies. What led us astray originally in our evaluation of longitudinal studies was the emphasis given to adaptive behavior and especially the psychology of learning. We were so concerned with the devising of standardized, reliable, and objective measuring instruments and with the formulation of generalizations concerning improvement in skills that we neglected the life histories of the laboratory animals which we inserted into the humanly determined measuring instrument. Individual differences in test-measured behavior were rarely deemed of interest except as they provided data for statistical exercise and, when they were mentioned, the term 'inherited' was used as a generic label rather than as the title of an hypothesis. Life histories of experimental animals were long neglected as laboratory data, and how individuals organized their interpersonal relations in their living cages prior to the experimental run in the maze was not seen as related to behavior in the maze.

One investigator has recently demonstrated that submission in a fighting situation in the living cage is related to nonrunning behavior in the maze.[10] This study indicates the value of complete information on animal behavior. Patterns such as mating and maternal activity were accepted as loosely determined genetic processes and studied mainly from the standpoint of drive strength. Analysis of sequences in the behavioral data and investigations of the meaning of the items in the behavioral pattern were largely omitted from consideration. Biologists, and especially ornithologists, however, paid some attention to these problems; but, even here, methodological considerations were minimized and crude observation sufficed as the bases of generalization.

To those fortunate few who have had the opportunity to study animal societies and individuals under natural conditions, the problem of the interrelationships between learning and genetic determination has been im-

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mediately apparent. On the one hand, field observations impress the participant with the generality, consistency, and apparent adaptiveness of certain behavioral forms. On the other hand, there are the frequent indications of variability, in the individual organism, of the elements in the generalized behavior pattern, as well as seemingly chance differences from individual to individual. For instance, in observing gestational behavior in many mammalian forms, one is brought face to face with the fact that the parturient mother almost invariably eats the after-birth up to, but not including, the offspring. That this behavior has been found in exclusively herbivorous animals, such as the guinea-pig, suggests a basis in tissue need rather than in an illy-conceived general label of inheritance. Furthermore, variations in the pattern from individual to individual have been noted. Some mothers do not stop with the placental tissue but continue to devour the young itself. Why does one find this pattern present in some mammals and absent in others, such as the fur seal, which has never been observed to eat after-birth material? The assumption that behavior of this invariant type within the species is genetically determined and "natural" for the species prevents the search for specific determinants which may or may not be acquired as a result of experience.

One can cite other examples of behavioral patterns which seem to be so adaptive and natural that they escape experimental notice. Martins[9] has recently pointed to the regurgitation of food by the nursing bitch of common household dog strains as a problem in psychological or physiological adaptation. To how many students of dog behavior has this been a research item? One seeks in vain for mention of the trait in descriptions of maternal behavior of dogs. So too, micturition patterns have remained almost unanalyzed except in so far as they touch on the problem of territoriality and dominance. What Lorenz and Tinbergen, among others, have pointed to is the necessity of making careful systematic analyses of these processes so that the evolution and ontology of behavior may be better understood.

In the light of the foregoing discussion, it is obvious that at least two lines of investigation are imperative if the history of any behavioral act is to become a matter of knowledge rather than of speculation. In the first place, presently existing criteria of innateness must be critically examined in order to make them experimentally useful. In the second place, techniques for isolating factors of learning and native behavior must be developed in such fashion that they can be used by the worker in the field as well as in the laboratory.

Criteria of Instinctive Behavior. Psychological literature has for a long time accepted three criteria for the determination of instinctive behavior.[5] The first postulates an instinct as existing when the behavior in question is universal. The second makes an instinct depend upon a specific biochemical or physiological mediator. The last of the usual criteria is based on phylogenic continuity of the observed datum. To these should be added a less explicit but none-the-less frequently invoked test of instinctiveness. This establishes an instinct as a behavior pattern which emerges in an animal isolated from its species mates so that imitation or social learning plays no part in the production of the pattern. Methodological weaknesses afflict all of these criteria. Universality would be a useful test were it not for the difficulty of arriving at a satisfactory sample population around which to build. Furthermore, even if one were able to observe all the members of a given species, one would also have to be able to describe the environmental conditions in such wise that it would be possible to rule out environmental constancy as a pervasive factor for the organisms studied.

For the field worker, the concept of universality is particularly dangerous. The problem of the uniqueness or the representativeness of the population observed is well-nigh impossible of solution. Other participants in this symposium have indicated the need for testing the reliability of the observer. The reliability of the sample is of equal significance. For illustrations of this point, one need but read any two descriptions by different naturalists of the same group. In trying to get some information on visual acuity in the Indian elephant, this divergence in observation was well brought out. One field student found the elephant to have remarkably keen vision. The other observer, working the same area and the same organisms, found them to depend almost wholly on nonvisual, sensory cues. We may assume both investigators to be equally careful observers. Were the animals sampled equally representative of the species? So, too, with ornithological descriptions of such phenomena as mating behavior in herring or laughing gulls. How reliable are findings that birds use the contrast of beak and chest colors as a stimulus for the breeding dance? How many observations are necessary, and under what variations in habitat and environment? In addition, the concept of universality is apt to blind the worker to the necessity of noting either small, but nevertheless significant, cultural or habitat differences or large, ever-present but ever-changing environmental constellations. As an illustration of this last point, Von Frisch[13] has recently demonstrated that the angle of the rays of the sun has an important stimulus value for dancing behavior in bees, and hence, an important effect on breeding and hive-making. The ever-present nature of the sun may have operated to have prevented the isolation of its effect as an important experimental variable before Von Frisch's study.

The second criterion, dependence on biochemical or physiological mediation, is more useful and in many respects the most fertile of the criteria advanced by psychologists. The difficulties encountered with this norm are much greater for the field worker than for the laboratory experimenter. To apply the criterion means for the field worker to interfere with the functional autonomy of the groups present in the field. Some writers on field methodology have implicitly or explicitly argued that it is the obligation of the naturalist to intrude as little as possible into the world of the observed species. If this contention prevails, the possibility of determining the history of a given act is limited to casual observation. What is required is a double period of observation, part with uninterrupted procedures and part with systematically varied interjection of the observer. As an illustration, endocrine level in ungulates has been raised by the injection of endocrine products from a distance.[15] Pellets of hormone have been shot into subjects in the wild with air-rifles or pistols. So, too, natural foods can be doctored and served to animals in their native habitats to determine the effect of specific products on the emergence of behavior patterns. Additional devices would include segregation of the young at an early age, surgical, chemical, or biological interference, and the return of the young to the native environment with periodic follow-up and study.

Biological continuity is a significant finding of relevance to the problem of instinctiveness only where it can be shown that such continuity is relatively independent of environment and is genetically controlled. Calvin Hall's study[3] of the inheritance of audiogenic shock tendency in mice is a case in point. By means of the selection of two strains of animals and the cross-breeding of generations of these organisms, it was found that this trait acted as though it were a unitary Mendelian characteristic. Lorenz[8] mentions some preliminary experiments in cross-breeding ducks to determine which of two allegedly innate patterns was genetically dominant. Sixteen clearly recognizable and nameable courtship acts were studied in several groups of ducks. Differences in patterning were established and hypothesized as innate. Cross-breeding of the two groups produced offspring with a mixture of the traits in question. These traits were presumable not morphologically formed; hence, the conclusion is drawn that they are natively determined. So too, Whitney[14] found that he could cross a strain of trail barking dog with another strain not showing this trait to obtain a breed showing a dominance factor for barking. Leopold[7] has presented evidence for the inheritance of tameness and wildness in the turkey. Methodology of this type is easily available to the psychologist, but a cautious approach is necessary so that good genetic procedures are used. The assistance of trained geneticists makes for good cooperative work in this area. Facilities such as zoological parks and collections are of invaluable assistance in providing species sufficiently related to make cross-breeding possible.

Of all the criteria advanced, that of isolation of the observed organism has seemed to be the easiest and most definite. The method involves separation of the young organisms as soon after birth as possible and, where possible, before actual parturition. The animal is then brought to any desired degree of maturation while isolated from its species mates. If the observed pattern of behavior appears, the conclusion is then drawn that that behavior is innate. The major difficulty with this standard lies in the actual or real meaning of the word isolation. Is isolation equivalent to the absence of species mates? Reflection will almost immediately establish the falsity of the equivalence.

It has been a commonplace of observation that organisms deprived of species mates of the opposite sex will, when mature and sufficiently deprived, engage in auto-erotic practices. Thus, the organism uses itself as a cage-mate surrogate. Its own body, in a sense, assumes the function of other members of the species. It is also possible that the experience of the organism with itself is a factor which conditions its later responses. In any event, isolation, when considered as separation from species mates, is not really conclusive for the appearance of instinctive behavior. Not only must the physical reality of the individual itself be taken into account, but also the inanimate *realia* of the environment.

It has frequently been reported that animals adopt reactive patterns to objects of the environment as if those objects were endowed with biological stimulating values. Thus, Thorpe[11] mentions the display of a budgerigar to a ping-pong ball. Hosking and Newberry[4] state that a great crested grebe, frightened from its egg-containing nest, left the eggs exposed and uncovered with the usual grasses. Upon return to the nest, the grebe went through motions identical with those used to uncover eggs although in this case the eggs were already completely exposed. Such findings raise important questions of interpretation. Was the uncovering of the eggs really the goal of the behavior reported? To what extent was the behavior an invariable response to any object within the environment? Only by knowing the genetic history of the organism's responses to the fixed objects of its environment can we determine the significance of the behavior in question. Perhaps, the bird uncovered the eggs as the result of long experience with concealed objects and therefore was not reenacting an instinctive action but simply responding to part of a conditioned stimulus.

It is impossible to discuss the present state of research on instinctive behavior without mentioning the point of view represented best by the writings of Lorenz and Tinbergen. European students of behavior have been particularly influenced by these workers and it is important to recognize both the strengths and the weaknesses of their contributions. Lorenz postulates a difference between what he calls instinctive behavior and the hard core of that behavior which is the instinct proper. This core, the *erbkoordination*, is an inborn movement pattern partaking of the nature of an automatism. The instinct in this sense is fixed, is more or less complex, and rests on endogenous stimulus production phenomena. These instinctive movements are independent of external stimuli and are already fully coordinated in the central nervous system. The data on which this view is based are drawn almost wholly from work with birds. The basic determinant is the invariability of the behavior studied and its teleological value for evolution and species-preservation. The independence of the instinct from external stimulation makes necessary the postulation of an energy phenomenon in the central nervous system which is reaction-specific.

This energy varies in some important respects from common chain-reflex energy concepts. In the first place, inhibition of the reaction results in a damming up of the energy, which in turn lowers the threshold for subsequent releasers of the instinctive act. Continued inhibition of the energy leads to a subsequent appearance of the instinctive behavior without any adequate stimulus for its appearance. This is the so-called "vacuum" response, the *leerlaufreaktion*. Many naturalists have been impressed by the appearance of such unstimulated behavior and have interpreted it as maladaptive or nonadaptive activity. An example of this energy accumulation activity can be cited from Fraser[2] who states that, in sheep, the ewe will frequently manifest maternal behavior toward a lamb despite the fact that her own offspring may be just about to be born. As soon as the lamb is delivered, attention is no longer paid to the other young. Lorenz[8] reports that young starlings go through the motions of fly-catching and killing although they have not ostensibly ever seen a fly before.

This independence from specific sensory stimulation is the hall-mark of an instinct whose basic energy has been accumulating somewhere in the central nervous system. Another mark of an instinct for Lorenz is that it is released but not guided by the environmental situation. The stimulus which acts as a releaser is, according to Lorenz, a receptor correlate. In other words, it is an aspect of the environment which is precisely specific for a certain type of response. Lack[6] showed that it was the few red feathers from a robin's breast which acted as a releaser for display or territorial defense in a live robin. These receptor correlates are hypothesized to be inborn.

To summarize the Lorenz scheme then, it postulates an instinct as a response to an innate releaser acting on an energy-system which in itself has certain unique characteristics, namely, accumulation, with subsequent self-release and self-lowered thresholds. The response called instinctive is an inborn movement response, often in the form of a chain reflex. The instinct forms a drive by its effect on the accumulation of energy which leads to the movement of the organism into an environment where a predetermined releaser, acting through the medium of a receptor correlate, relieves the tension caused by the accumulation of energy.

In justice to Tinbergen, it should be stated that he is not completely in accord with the concepts described in the foregoing paragraphs. In his recent article,[12] he emphasizes the necessity of careful examination of the nature of the "releaser." His own experimental researches give evidence of the fruitfulness of the method of using artifacts to enhance and isolate various aspects of what he terms the "sign stimulus." Tinbergen also stresses the place of conditioning in determining the stimuli to which the organism responds.

The Longitudinal or Life-History Method. The foregoing rather lengthy examination of current viewpoints on the criteria for the isolation of factors of learning and instinct would be of little purpose if it did not lead to a consideration of techniques and methods for arriving at definite statements of fact of a noninterpretative sort. In the first place, it is obvious that, for both the field and the laboratory worker, the understanding of a given behavioral phenomenon becomes a function of its history in the life sequences of the individual. This functional relationship to the development of the individual is not merely a statement of physiological or behavioral maturation. By history is meant the total interreaction of the organism with its environment. In the search for environmental factors of relevance to the emergence of a behavioral pattern, not only must the observer be alert for minute variables, he must also take into account those all-pervasive features of the *milieu* which so often escape notice. In discussing tissue needs, for instance, the usual treatment lists thirst, hunger, and sex as biological demands. One might well inquire why the need for oxygen or air has been omitted. Perhaps the all-embracing nature of the need has made for the omission. Von Frisch's discovery of the effect of the sun's rays is of this nature. The inquirer into behavior who utilizes the longitudinal method must be aware of all such items.

What are the characteristics of the longitudinal approach which must be attended to in order to utilize it in both the field and the laboratory? The taking-off place for both workers lies in the careful observation of the processes and behaviors involved in the inception of the activity of the individual. In most instances, this means systematic attention to mating, gestational, and maternal-paternal behavior. Systematic attention likewise has implications for research workers. There are any number of factors which can be systematically varied. For instance, we have pointed to the lack of a purely vegetarian diet among herbivorous mammals. Supplying of meat to pregnant, non-meat eating organisms might provide a clue as to the nature of the hunger for the afterbirth. In a preliminary study with the white rat at the Museum of Natural History, pregnant and nonpregnant females were provided with various breakdown elements of meat, aminos, undifferentiated protein, non-nutritious roughage, salts, *etc.* The pregnant animals appear at this time to differ more significantly in salt consumption than in other aspects of their diet. In Martin's observation of pregnant guinea pigs, also made at the Museum, there was a significant preference for meat by pregnant females as compared to other groups of guinea pigs. Continued analysis of food preferences with finer subdivisions among the elements offered may help to explain the variations in this part of the maternal relationship from both individual to individual and species to species. Perhaps the absence of placental eating in the fur seal is a result of diet rather than of the so-called "instinctive" equipment of the organism.

Another illustration of the effects of careful study of environmental factors on determination of the origin of instinctive behavior comes from an investigation of maternal care in the rat. One of the commonly described concomitants of maternalism in this animal is nest building. In an as yet incomplete study, it has been discovered that animals bred without access to manipulatable objects, including food, were found not to build nests during or after pregnancy. Nest-building behavior is then only in part a product of normal, species-determined factors. It is also in part the result of acquired reactions to and with objects in the environment.

Retrieving and suckling of the young are likewise much more complicated acts than has been assumed to be the case. In studies now under way at the American Museum and City College, Birch and his collaborators have undertaken to utilize the method of isolation with a realization of the implications therein contained. They have with great ingenuity devised a technique for isolating one part of the organism from the rest of its own body. A piece of soft rubber fastened around the neck serves as an Elizabethan ruff to prevent the female from acquiring any experience, olfactory, gustatory, or visual, of its own genitalia. Attached at the time of weaning, the ruff was effective in abolishing normal nursing behavior in the animals so treated when they had given birth to pups after the ruff had been removed shortly before gestation. The application of this methodology by the field worker presupposes the interference of the observer in the life history of the species observed. It should be possible, under some circumstances, to remove natural environmental stimuli or to substitute carefully prepared artifacts for them.

Apart from considerations of the inanimate environmental constellation, there are the species-mate relationships which must be examined developmentally. At the New York Zoological Park in the Bronx, we were fortunately able to study the ontogenesis of social relations in the gibbon. Carpenter[1] has described this primate as a highly developed familial animal. From field observations in Thailand, it was apparent that, under natural habitat conditions, the amount of interpersonal relationship among members of gibbon families was great. At the Zoo, a group of three animals was observed on an island under conditions which, in general, paralleled free ranging life. The group consisted of father, mother, and two-year old young. A significant difference was established in familial contacts as contrasted to Carpenter's animals. The amount of interindividual relationship was at a minimum. One year later, when a newly-born gibbon was added to the group, family cohesiveness was much greater. It seems at least a plausible hypothesis that the family organization in this species is partly dependent upon population pressure. Such studies utilizing the opportunities afforded by zoological collections can be multiplied with tremendous gain to the understanding of animal behavior.

Lorenz has pointed out the value of using artifacts to identify the aspects of the stimulus situation which serve as releasers for the behavior in question. As indicated above, Lorenz's theoretical position on instincts does not invalidate the utility of the methods he has employed. Presentation of model animals with carefully selected and enhanced parts is valuable as a method of identifying the items to which an organism responds. It does not, however, answer the question as to the innateness or acquired nature of a response. That immature penguins respond to the corner of the beak of female as the initiator of a regurgitation-feeding process does not explain how this behavior originates. Once the releaser is identified, however, the problem of origin is pointed up and made more susceptible to experimental attack. The method of experimental group formation may provide an answer to problems like the above. Selection of a newly hatched penguin and its incorporation in a family group where the beak has been variously painted or stripped of surrounding feathers will reveal the extent to which environmental factors are responsible for the behavior. Hormonal implantation to insure more rapid maturation of the young will also be of help in determining the sequence of events. The combination of these various methods of attack is probably the best solution to the whole problem.

In conclusion, it can be said that the longitudinal method is basically useful for the isolation of facts of learning and native behavior. It must be kept in mind, however, that this approach entails a double responsibility on the observer. He must be as aware of the relevance of all aspects of the environment as he is of the so-called "psychological" factors within the organism. Willingness to interfere with the organization of the group activities of the species observed must be tempered with periods of observation of the untampered-with life histories. Hormonal, dietary, and artifactual controls are possible both in the wild and in the laboratory. What is really the heart of the method is the freedom of the experimenter from implicit or explicit biases which deflect attention and methodology from all the varied aspects of the behavior to be isolated. Finally, the experimenter must be alert against the tendency to solve his problems by assuming what he is trying to demonstrate. Thus, calling an action innate because it seems to be natural is not a conclusion but an hypothesis.

Summary. Three criteria for differentiating between "native" and "acquired" behavior have been advanced by psychologists. The first holds that a biologically prevalent or "universal" behavior pattern is *ipso facto* native. The second maintains that traits varying independently of the cultural or social environment are inherited. Finally, traits are held to be "unlearned" when the animal demonstrating them has been separated from his species mates at a time prior to the appearance of the traits. The first two criteria have long been accessible for use in field observations. The third has usually been relegated to the area of laboratory studies. In most instances, however, the criteria have been employed without much scrutiny of the methodological implications inherent in them. "Universality" has been applied to large, generalized behavior patterns as well as to smaller segmental elements without recognition of the need for determining whether environmental pressures of biological intraorganismic factors were causal. So too, independence from the environment has been applied loosely to major aspects of the *milieu* and uncritically generalized to specific behavior. Isolation has been generally misconceived to imply that isolation from the environment is synonomous with separation from species mates. Recent field observations at the New York Zoological Society and studies in the Department of Animal Behavior at the American Museum of Natural History illustrate newer means of isolating the relevant factors.

References

1. Carpenter, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon (*hylobates lar*). Comp. Psychol. Monogr. **16:** 1–212.
2. Fraser, A. 1937. Sheep Farming. Crosby Lockwood. London.
3. Hall, C. S. 1947. The genetics of audiogenic seizures in house mice. Amer. Psychologist **2:** 349.
4. Hosking, E. & C. W. Newberry. 1944. Birds of the Day. London.
5. Klineberg, O. 1940. Social Psychology. Henry Holt. New York.
6. Lack, D. 1939. The behavior of the robin. Part II. A partial analysis of aggressive and recognitional behavior. Proc. Zool. Soc. (London) **109:** 200–219.
7. Leopold, A. S. 1944. Nature of heritable wildness in turkeys. Condor **46:** 133–197.
8. Lorenz, K. 1939. Vergleichende Verhaltensforschung. Zool. Anzeig., Suppl. Bd. **12:** 69–102.
9. Martins, T. 1948. Regurgitation in female dogs. (Film) Amer. Mus. Nat. History.
10. Riess, B. F. 1946. Freezing behavior in rats and its social causation. J. Soc. Psychol. **24:** 249–251.

11. THORPE, W. H. 1948. The modern concept of instinctive behavior. Bull. Anim. Behav. **7:** 1–12.
12. TINBERGEN, N. 1948. Social releasers and the experimental method for their study. Wilson Bull., **60**(1): 6–52.
13. VON FRISCH, K. 1947. The dances of the honey-bee. Bull. Anim. Behav. **5:** 1–22.
14. WHITNEY, L. F. 1929. Heredity of the trail barking propensity in dogs. J. Hered. **20:** 561–562.
15. WISLOCKI, G., J. AUB, & C. WALDO. 1947. The effect of gonadectomy and testosterone proprionate on the growth of antlers in male and female deer. Endocrin. **40**(3): 202–224.

TECHNIQUES FOR OBSERVING BIRD BEHAVIOR UNDER NATURAL CONDITIONS

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An undisturbed natural habitat is the proper place to study natural behavior. Such habitats were the laboratories of the old-time naturalists who observed by simple direct techniques and recorded their findings in anecdotal form, drawing conclusions as warranted by inductive reasoning. In spite of the errors and fanciful situations which they occasionally reported, these naturalists laid the foundation for our modern science of animal behavior.

The present outlook and approach is basically unchanged, although modern techniques have widened the scope of field studies and modern scientific standards have placed new demands for accuracy and caution. Experimental procedures have been introduced, capable of measuring and analyzing phenomena which formerly were reported only in general descriptive terms.

Work with captive birds in the laboratory has made it possible to study and analyze certain details of behavior which are beyond the reach of the field investigator; but studies made in nature still provide and will continue to provide many fundamental principles and hypotheses of natural behavior.

The present paper attempts to survey the various techniques and tools used in observing bird behavior in the field. These techniques and tools are common knowledge to many, and their enumeration may seem unnecessary. The writer, however, knows of no compilation of this sort, and believes that it may be of some value as a reference for field workers and as an indicator of the problems and methods of modern field research for laboratory scientists who recognize the importance of the study of animals in nature. The term "bird behavior" is here restricted to the various aspects of individual and social behavior and excludes problems of population behavior. The references to literature are intended to provide illustrations and suggestions for further reading rather than an exhaustive bibliography.

Three principal approaches are employed in the modern study of bird behavior under natural conditions. These are: (1) direct observation, (2) indirect observation, and (3) experimental analysis.

Direct Observation

Since the central objective in these studies is an understanding of natural behavior, it is appropriate that considerable attention be given to techniques which aid in the direct observation of birds under strictly natural conditions. Of course, the very interjection of the observer into the scene constitutes *a priori* a disturbance of the natural conditions. A major concern of the field worker thus becomes the development of tools and techniques which will aid him in his direct observations and at the same time minimize any disturbance which may be created by his presence. Such tools and techniques may be classified under three headings: (*a*) optical and mechanical aids, (*b*) blinds, and (*c*) lures and decoys.

(*a*) *Optical and Mechanical Aids*. A small binocular field glass magnifying about six diameters is the most important single tool of the field ornithologist.[1,2] It is to him what a microscope is to the laboratory worker. Through magnification and a narrowing of the field of distraction it permits him to follow the actions of a bird closely at distances sufficient to minimize or nullify the effect of his presence.

An instrument of higher magnification has obvious advantages for work at long distances, but has inherent disadvantages in the form of weight, limited field, and reduced illumination. Monocular spotting scopes (terrestrial telescopes) of from fifteen to thirty-five power are commonly used for identifying water fowl and other birds in open areas. For the prolonged observation periods required in studies of bird behavior, however, a binocular instrument is distinctly preferable.[3] Such instruments must be mounted on a sturdy tripod or other brace and, as a consequence, are of greatest value at fixed observation stations.

Illumination is an important limiting factor with all field glasses. Unable, under usual circumstances, to throw artificial illumination on his subject as does the microscopist, the field ornithologist must depend on the light gathering capacities of his instrument. Large objective lenses in combination with a relatively low magnification assure maximum brightness of the image.[4] The new process of lens coating serves to further increase the light transmission by about 50 per cent and at the same time reduces glare.[5] Observations of nocturnal species require artificial illumination. Ordinary white light of low intensity may not be disturbing, but in situations where invisible light would be preferable, observations may be made with a snooperscope under infrared illumination.[6]

The airplane should be mentioned as a mechanical aid in bird observation. With its use, special studies have been made of flocking behavior in waterfowl[7] and of homing flights in gannets.[8] In another medium, diving gear has made it possible to observe the underwater behavior of diving birds.

(*b*) *Blinds*. Most birds will, after a short period of adjustment, completely accept the presence of a new inanimate object in their home range. It is thus possible to erect tents or other similar structures which can provide concealed observation posts at positions convenient for watching behavior. In this way the observer can lift himself into the intimate home circle of a bird and there study its behavior undetected, at close range.

Blinds or hides have been familiar tools of the hunter for many centuries. Their adaptation to studies of bird behavior in the hands of bird students and nature photographers was largely a development of the early years of the present century.[9,10] The form of a blind can, and often must, be varied according to the situation and the species under observation. Almost any structure will do that provides a complete screen and a comfortable seat for the observer. Where an easily constructed, portable blind is needed, ornithologists have used packing boxes, pup tents, burlap or canvas-covered crates, and a wide variety of contraptions involving umbrellas, snow fencing, hog-wire fencing, or specially prepared rods as support, with canvas, burlap, tarpaper, or artificial grass matting as covering. The details of construction are unimportant so long as the blind provides the necessary screening, is comfortable and adequately ventilated for extended periods of watching, and is sturdy enough to withstand the elements. Light weight, ease of transporting, and ease of erecting and dismantling are often additional factors of importance. Transparent or "one-way" mirrors are valuable in some situations, but a simple slit or peep-hole with or without a zipper is usually adequate and satisfactory.

Special situations call for special structures. The use of towers was demonstrated by Herrick in his studies of eagle behavior.[11] Smaller wooden towers have been used with outstanding success in studies of night herons,[12] willets,[13] and of various marsh and prairie birds at the University of Wisconsin. Tree houses reached by rope ladders and suspended seats raised and lowered by block-and-tackle have been used in treetop studies in the tropics.[1,14]

Mobile blinds are of great value in studies of wide-ranging species which do not regularly visit areas on which a blind can be conveniently erected. Early naturalists occasionally employed the hunter's technique of stalking game behind specially trained horses or cattle or of disguising themselves as animals.[15] Detailed and extended observation, however, requires a comfortable screened enclosure such as that provided by a trailer[16] or by a small automobile equipped with appropriate curtains. Automobiles are, of course, limited as to where they can go, but, in at least a few studies, their use has proved feasible.[17] Towers on wheels have been suggested for studies in tropical forests.[1]

Once constructed, a blind is easy to use. Birds vary in the speed and completeness with which they will accept a blind; and the position of a blind with respect to a nest, a feeding ground, or a courtship ground must be varied accordingly. In many instances, it is necessary to enter a blind before daybreak or to employ one or more colleagues to accompany the observer to the blind and then leave so that the bird may see the departure.

(*c*) *Lures*. The natural physical or social appetites of wild birds may be exploited to bring them into the observation range of the bird student as he is ensconced in a blind. It is true that the use of lures and decoys injects an unnatural element, but, with full recognition of this limitation, there are situations and problems for which the technique is justified and decidedly useful.

Feeding and watering stations provide one of the simplest and most effective types of lures.[2] The concentration of food or water near a convenient blind not only brings the birds to the observer, but locally intensifies the competition among the birds visiting the station so as to precipitate features of behavior which might otherwise remain obscure and undetected.[18] In the same way, bird houses[2] or nesting platforms[19] are effective in inducing birds to nest in situations suitable for close study. In a special technique, birds are held in convenient flight cages until they have started to nest, after which the doors are opened and freedom is granted, limited only by the instinctive responses of the birds to the established nest site.[20]

Calls and effigies in imitation of a bird's familiar associates are useful devices for luring birds to the observer. Imitations of the song, of alarm notes, or, especially, of distress calls will often bring a prompt response. The squeaking noise produced by noisily kissing the back of the hand in imitation of the distress call of a young bird is effective for many species especially during the breeding season. The effect of such sounds is generally transitory, however, and the technique is useful primarily as a means of inducing shy birds to reveal themselves briefly for identification.

Living birds or artificial replicas of birds may be successfully used as decoys in many situations and with many species.[21,22] The decoy selected usually corresponds to the species under study, but other types, particularly predatory birds and mammals, may bring a definite response.[23] Artificial decoys commonly lose their effectiveness after the initial encounter and are thus of limited value in luring birds to an observer for behavior studies. Living decoys on the other hand, particularly if they are relatively unrestricted, may be highly effective in holding, or repeatedly luring, wild individuals to the observer's blind.[24]

It must be emphasized that decoys operate on the social appetites of birds and thus induce a specific social response. When used in behavior studies, they must generally be regarded as experimental tools rather than as simple lures.

Markers for Identifying Individuals. The detailed study of a bird society by direct observation requires a means of individually differentiating the members of that society for quick recognition. Natural individual variations in appearance or behavior have been used successfully for distinguishing the members of a flock,[25] but, in general, it is dangerous to rely on such characters. Each bird must accordingly be tagged with a marker which is (*a*) conspicuous, (*b*) durable, (*c*) non-irritating to the bird, and (*d*) applicable in sufficient variety to provide an adequate number of distinctive combinations. The marking of wild birds generally involves trapping or netting. For trapping techniques, the reader is referred to the U. S. Government's bird banding manual.[26]

A variety of artificial markers have been devised for field studies. Each of these has special advantages for certain situations, and the worker must select and devise according to his special needs. A few types are here described as an indicator of the problems involved in marking birds and the solutions which have been devised in meeting them.

Colored leg bands have been used sporadically since the time of Audubon[27,28] and systematically in behavior studies of wild birds since about 1930.[29,30] They have proved to be relatively durable, harmless markers applicable in a considerable assortment of colors and color combinations and are reasonably conspicuous on species which expose their tarsi to view. Metal bands, painted or stained, have been used in several studies, but celluloid bands are generally favored, the coil type or butt-end type being preferable to the spiralled bands commonly used on poultry.

Colored body or wing markers are generally less permanent than leg bands but have a special value on species which commonly hide their legs from view. Stains and dyes have been used on many species and are particularly successful when applied to white plumage.[31,32] Recent improvements in dyeing the plumage make it possible to follow individual birds in the field for as much as six months.[33] Paints and lacquers which mat the feathers are unsatisfactory on the body plumage but may be applied to individual wing feathers[34] or tail feathers (see below). Birds must generally be trapped for marking, but paints and dyes have been applied in special situations by placing an applicator at a nest entrance or other passage or by spraying,[35] the form of the random pattern on each bird being used as the distinctive individual marker. Shoulder tags of coroseal, attached through the loose skin between the shoulders so as to hang on either side of the breast were successfully used in one study of pheasants,[36] and a few preliminary tests suggest the usefulness of coroseal collars with tabs hanging on either side of the breast.

Colored tail markers are particularly useful for quick identification of birds as they are flushed. Straight or upcurled white feathers, dyed in various colors, have been used, applied to the rectrices with glue[37] or with a double-pointed needle set in the clipped feather base.[38] Fast-drying lacquer paint or airplane dope applied individually to the rectrices, so as to avoid matting, has proved satisfactory on several species,[39] especially when applied as a double coat. Showy tags of a plastic material, pyralin, clipped to the tails of pheasants can provide a considerable variety of color combinations.[40]

The contour of a flying bird may be modified in a small variety of patterns by selectively trimming tail and wing feathers. This method, particularly useful for soaring birds or for "hawking" species, can be exploited only to a limited extent without interfering with flight and is primarily useful in separating population units such as sex groups, age groups, or the members of neighboring flocks.

Indirect Observation

The examination and interpretation of "signs" and other by-products or evidence of bird activity is of value as a means of obtaining information on problems which cannot be attacked by direct observation or which would require an unreasonable amount of watching and waiting. Thus, the close examination of a bird's nest provides information on the activity that went into its construction. Data on eggs and young similarly shed light on various aspects of reproductive behavior. Counts and plottings of tracks in snow or dust may furnish clues on the grouping and movements of terrestrial birds,[41] accumulations of droppings provide information on gregarious roosting habits and habitat selection, while simple counts of birds visiting a feeding station may be used in analyzing the ecological association between species.[42] Much of our information on feeding behavior, as well as food habits, has come through the analysis of droppings, pellets, and stomach contents. Data obtained by these indirect means cover only a few limited aspects of bird behavior, but they have a special significance in their objectivity and their quantitative nature.

A number of special tools and techniques have been devised for recording the activity of free-living birds. The feeding of dyes at bait stations provides a means of studying flock ranges through the search for colored feces at roosting and loafing sites. The setting out of distinctively marked sticks and strings has contributed to an understanding of how and where birds collect materials for nest construction,[43] and the marking of eggs has furnished data on the frequency of turning by the incubating bird.[44] Recording devices have been used with thermometers to analyze the activity of birds at their nests,[45] with vibrometers to measure heart and respiration rates[46] and with Geiger counters to record the exact time of return of radioactively tagged birds in homing experiments.[47] Photography,[48] particularly high-speed flash photography[49] and slow-motion cinematography,[50] is a recording technique useful in measuring and analyzing bird behavior which is too fast or too complicated to be perceived in its entirety by direct observation.

Experiments in the Field

Direct and indirect observations of birds under natural conditions have suggested numerous principles and hypotheses which may be checked and analyzed by experimental procedures. By bringing birds in from the field and confining them under conditions of close control, much has been learned of physiological and certain psychological phenomena, but most measurements of natural behavior and determinations of the natural conditions of their existence cannot be made under conditions of confinement. If experimental procedures are to be applied to these problems, they must be applied in the field under essentially undisturbed conditions.

Experiments with free-ranging birds under the highly variable and uncontrollable environment of the field are fraught with difficulties and pitfalls. In the first place, the experimental subjects are difficult to capture for marking and for treatment. After they have been returned to their natural environment, they are evasive and difficult to follow. Many individuals, prepared at great expense of time and effort, are never seen again. And, finally, the physical environment, so nicely regulated in modern laboratories, is completely beyond the control of the field experimentalist.

In spite of these obstacles, the experimental study of bird behavior in the field holds great promise. The problem of environmental regulation is surmounted by the use of controls. In field experiments with birds, the controls are the undisturbed, free-living birds in nature, exposed, so far as can be determined, to the same environmental forces as the experimental birds, with the single exception of the special factor applied in the experiment. Sometimes these controls comprise flock mates or neighboring individuals. In other cases, they are the same birds or other residents of the experimental area, observed during previous and/or succeeding seasons.

Experimental procedure in a broad sense has been described as the observation of phenomena under conditions manipulated and controlled by the investigator. In field studies, it is occasionally possible to utilize occurrences of a purely natural but unusual phenomenon in the same way as an experimental manipulation. Thus, the occurrence of a solar eclipse can be utilized for analyzing the responses of free-living birds to the irregular appearance of darkness. The alert field investigator takes advantage of phenomena of this sort as they appear, and of man-made changes of environment such as those resulting from agriculture, lumbering, and drainage, changes which would be too expensive to undertake directly for experimental purposes but which, if anticipated, can often be used to the same end.

Experiments with free-living birds generally fall into one of three classes, depending on whether they are concerned with factors of (*a*) the physical environment, (*b*) the social environment, or (*c*) the internal environment.

(*a*) Experimental manipulations of the physical environment are usually directed toward an analysis of the food and cover relations of a species or the effects of special features of the environment, such as nests and nest contents on social and reproductive behavior. Quantitative manipulations of food have been shown to affect the social reactions of birds as the population responds by concentrating or dispersing.[51] Multiple choice experiments have provided interesting and useful information on such phenomena as food preferences,[52] cover preferences,[53] nest hole recognition,[54] and color discrimination.[55,56] The relationship of nests and their contents to bird behavior has been shown by experimentally manipulating the position of nests,[9,57] the construction of nests,[58,59] and the nest contents.[57,58,60] The importance of prominent landmarks in a bird's familiar surroundings on its behavior has been demonstrated in experiments which drastically alter these features[61] or which transplant the bird to new and unfamiliar surroundings.[62,63] Studies of orientation and homing have utilized the experimental procedure of transporting birds under various conditions and then noting,[64] timing,[65,66] or directly tracing[8] their subsequent flight.

(*b*) Experiments designed to evaluate and analyze the social environment are concerned with the influence of intra- and extra-specific associates on a bird's behavior. The reactions of individual birds in the presence of unfamiliar associates have been studied by transporting them to areas populated by others of the same species,[63] by placing caged birds in occupied nesting territories,[67] and by the use of mirrors.[67] (A bird's own image is, of course, unfamiliar to it.) Stuffed dummies and decoys are, in a sense, unfamiliar associates, and their use has proved valuable in many studies of the social responses of free-living birds, particularly in analyzing sex recognition and sex behavior.[68,69] The significance of various features of a bird's form and pattern as releasers for social and sexual behavior has been studied experimentally through distortions of plumage[70,71] and through the use of dissociated parts of a bird.[72,73]

(*c*) Experiments on the internal drives and physiological processes which underlie overt behavior reactions are generally difficult to conduct in the field. The study of the effects of drugs on the behavior of free-living birds is a promising but unexplored field. Complicated neurological and endocrine techniques are hardly feasible on subjects which are to be turned out into the highly competitive and dangerous outdoor environment. Castration, however, is a simple operation in male birds, and has been employed in a few field studies.[74] Experiments involving the injection of hormones and other substances have been impractical for field studies until recently, because of the necessity for repeated handling of the subject. The development of the hormone pellet technique,[75] however, has opened up new opportunities for field experimentation.[76] Several investigators have stimulated sexual activity in wild birds by exposing them to artificial day lengths in captivity and subsequently releasing them, following their movements in so far as possible during the ensuing weeks.[77, 78] The writer knows of no experiments in which free-living birds were exposed to controlled artificial day length, although one study analyzed a parallel situation wherein roosting starlings were incidentally exposed each night to the illumination of a lighted city street.[79]

Summary

Free-living birds existing in natural environments constitute the best material for studies of bird behavior. Direct and indirect observations of undisturbed birds furnish data and suggest hypotheses which may then be checked and analyzed by field experiments. The present paper surveys the principal techniques and tools used in studying bird behavior in the field, including optical aids, blinds, lures and decoys, the reading of signs, the use of recording instruments, and the employment of experimental procedures.

Bibliography

1. Nicholson, E. M. 1932. The Art of Bird Watching. Scribners. New York.
2. Baker, J. H. 1941. The Audubon Guide to Attracting Birds. Halcyon House. Garden City, New York.
3. Chapman, F. M. 1929. My Tropical Air Castle. D. Appleton Co. New York.
4. Reichert, R. J. & E. Reichert. 1948. Choosing a binocular. The Amer. Rifleman.
5. Reichert, R. J. & E. Reichert. 1946. These hard-coating jobs. The Amer. Rifleman.
6. Morton, G. A. & L. E. Flory. 1946. An infra-red image tube and its military applications. RCA Review **7:** 385–413.
7. More Game Birds in America. 1936. The 1935 international wild duck census. More Game Birds in Amer. Fnd.
8. Griffin, D. R. & R. J. Hock. 1948. Experiments on bird navigation. Science **107**(2779): 347–349.
9. Herrick, F. H. 1902. The Home Life of Wild Birds. Knickerbocker Press. New York.
10. Allen, A. A. 1930. The Book of Bird Life. D. van Nostrand Co. New York.
11. Herrick, F. H. 1924. An eagle observatory. Auk **41:** 89–105.
12. Allen, R. P. & F. P. Mangels. 1939. Studies of the nesting behavior of the black-crowned night heron. Proc. Linn. Soc. N. Y. 1938–1939, Nos. 50, 51.
13. Vogt, W. 1938. Preliminary notes on the behavior and ecology of the eastern willet. Proc. Linn. Soc. N. Y. **49:** 8–42.
14. Hingston, R. W. G. 1932. A Naturalist in the Guiana Forest. Longmans, Green & Co. New York.
15. Branch, E. D. 1929. The Hunting of the Buffalo. D. Appleton Co. New York.
16. Bailey, G. A. 1922. The trailer-blind de luxe. Bird Lore **24:** 323–327.
17. Emlen, J. T. 1939. Seasonal movements of a low-density valley quail population. J. Wildl. Man. **3:** 118–130.
18. Collias, N. & R. D. Taber. 1948. Grouping and dominance relations among wild ring-necked pheasants. Anat. Rec. (suppl.) **101:** 44–45.
19. Calhoun, J. B. 1948. Utilization of artificial nesting substrate by doves and robins. J. Wildl. Man. **12:** 136–142.
20. Ivor, H. R. 1944. Bird's fear of man. Auk **61:** 203–11.

21. Heilner, V. 1939. A Book on Duck Shooting. The Penn Publ. Co. Philadelphia, Pa.

22. Nichols, J. T. & F. Harper. 1916. Field notes on some Long Island shore birds. Auk **33:** 237–255.

23. Bolles, F. 1890. Barred owls in captivity. Auk **7:** 101–114.

24. Ter Pelkwyk, J. 1941. Fowling in Holland. Bird Banding **12:** 1–6.

25. Jenkins, D. W. 1944. Territory as a result of despotism and social organization in geese. Auk **61:** 30–47.

26. Lincoln, F. C. 1929. Manual for bird banders. U. S. Dept. Agric. Misc. Publ. 58.

27. Audubon, J. J. 1827–38. The Birds of America. Vol. 1: 227. London.

28. Gain, L. 1912. Penguins of the Antarctic regions. Rept. Smith's Inst. 1912: 475–482.

29. Butts, W. K. 1930. A study of the chickadee and white-breasted nuthatch by means of marked individuals. Bird Banding **1:** 149–168.

30. Hickey, J. J. 1943. A Guide to Bird Watching. Oxford Univ. Press. London.

31. Watson, J. B. & K. S. Lashley. 1915. An historical and experimental study of homing. Papers, Dept. Marine Biol. Carn. Inst. Wash. **7:** 1–60.

32. Price, J. B. 1931. An experiment on staining California gulls. Condor **33:** 3.

33. Wadkins, L. A. 1948. Dyeing birds for identification. J. Wildl. Man. **12:** 388–391.

34. Wandell, W. N. 1943. A multi-marking system for ring-pheasants. J. Wildl. Man. **7:** 378–382.

35. Moffit, J. 1943. Marking by spurts of dye. J. Wildl. Man. **6:** 312–318.

36. Taber, R. D. 1948. Observations of the breeding behavior of ring-necked pheasants. Condor **51:** 153–175.

37. Baumgartner, A. M. 1938. Experiments in feather marking eastern tree sparrows for territory studies. Bird Banding **9:** 124–135.

38. Wright, E. G. 1939. Marking birds by imping feathers. J. Wildl. Man. **3:** 238–239.

39. Staebler, A. E. (Unpublished data communicated at the 29th annual meeting of the Wilson Ornithological Club in Columbus, Ohio, November, 1947.)

40. Trippensee, R. E. 1941. A new type of bird and mammal marker. J. Wildl. Man. **5:** 120–124.

41. Errington, P. L. & F. N. Hammerstrom. 1936. The northern bobwhite's winter territory. Iowa State Coll. Agr. & Mech. Arts., Res. Bull. 201.

42. Dice, L. R. 1948. Application of statistical methods to the analysis of ecological association between species of birds. Amer. Midl. Nat. **39:** 174–178.

43. Williams, H. S. 1939. The Private Life of Birds. McBride. N. Y.f

44. McCabe, R. A. & A. S. Hawkins. 1946. The Hungarian partridge o Wisconsin. Amer. Midl. Nat. **36:** 1–75.

45. Kendeigh, S. C. & S. P. Baldwin. 1930. The mechanical recording of the nesting activities of birds. Auk **47:** 471–480.

46. Odum, E. P. 1941. Variations in the heart rate of birds: a study in physiological ecology. Ecol. Monogr. **3:** 299–336.

47. Griffin, D. (Unpublished data.)

48. Schwartz, C. W. 1944. The prairie chicken in Missouri. Cons. Comm., Mo.

49. Allen, A. A. 1948. New light dawns on bird photography. Nat. Geogr. Mag. **93:** 774–790.

50. Queeny, E. M. 1946. Prairie Wings. Ducks Unlimited Inc. New York.

51. Hamerstrom, F. 1942. Dominance in winter flocks of chickadees. Wils. Bull. **54:** 32–42.

52. Hawkins, A. S. 1937. Winter feeding at Fayville Grove. Amer. Midl. Nat. **18:** 417–425.

53. Buss, I. O. 1942. A managed cliff swallow colony in southern Wisconsin. Wils. Bull. **54:** 153–161.

54. Von Haartman, L. 1944. Die orientierung des Trauerfliegenschnäppers, *Musciapa h. hypoleuca* (Pall), zum Nesteingang in einem Nistkasten mit mehreren Öffnungen. Ornis Fennica **21:** 69–89.

55. Pickens, A. L. 1935. Studies in avian color reaction. Condor **37:** 279–281.

56. Kalmbach, E. R. 1943. Birds, rodents and colored lethal baits. Trans. 8th N. Amer. Wildl. Conf: 408–416.

57. Noble, G. K. & D. S. Lehrmann. 1940. Egg recognition by the laughing gull. Auk **57**: 22–43.

58. Emlen, J. T. 1941. An experimental analysis of the breeding cycle of the tricolored redwing. Condor **43:** 209–219.

59. Dubois, A. D. 1923. An experiment with a rufous hummingbird. Condor **25:** 157–159.

60. Kirkman, F. B. 1937. Bird Behavior. T. Nelson & Sons. New York.
61. Watson, J. B. 1908. The behavior of noddy and sooty terns. Pap. Tort. Lab., Carn. Inst. **103:** 187–255.
62. McCabe, R. A. 1947. The homing of transplanted young wood ducks. Wils. Bull. **59:** 104–109.
63. Howard, W. E. & J. T. Emlen. 1942. Intercovey social relationships in the valley quail. Wils. Bull. **54:** 162–170.
64. Yeagley, H. L. 1947. A preliminary study of a physical basis of bird navigation. J. Appl. Physics **18:** 1035–1063.
65. Rüppell, W. 1936. Heimfindeversuche mit Staren und Schwalben. 1935. J. f. Orn. **84:** 180–198.
66. Lockley, R. M. 1942. Shearwaters. J. M. Dent & Sons. London.
67. Allen, A. A. 1934. Sex rhythm in the ruffed grouse, (*Bonasa umbellus* Linn.) and other birds. Auk **51:** 180–199.
68. Noble, G. K. & W. Vogt. 1935. An experimental study of sex recognition in birds. Auk **52:** 278–286.
69. Mason, A. G. 1941. Further experiments with corncrakes. Irish Nat. J. **7:** 321–333.
70. Noble, G. K. & M. Wurm. 1942. Further analysis of the social behavior of the black-crowned night heron. Auk **59:** 205–224.
71. Noble, G. K. 1936. Courtship and sexual selection of the flicker (*Colaptes auratus luteus*). Auk **53:** 269–282.
72. Lack, D. 1939. The behavior of the robin. Parts 1 and 2. Proc. Zool. Soc. London, Ser. A, Vol. 109, pts. 2 and 3: 169–219.
73. Goethe, F. 1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus a argentatus Pontopp.*) auf der Insel Memmerstand. J. f. Orn. **85:** 1–119.
74. Hann, H. W. 1939. The relation of castration to migration in birds. Bird Banding **10:** 122–124.
75. Deansely, R. & A. S. Parkes. 1937. Factors influencing effectiveness of administered hormones. Proc. Roy. Soc. London **124B:** 279–298.
76. Emlen, J. T. & F. W. Lorenz. 1942. Pairing responses of free-living valley quail to sex hormone pellet implants. Auk **59:** 369–378.
77. Rowan, W. 1929. Experiments in bird migration. I. Manipulation of the reproductive cycle: seasonal histological changes in the gonads. Proc. Boston Soc. Nat. Hist. **39:** 151–208.
78. Wolfson, A. 1940. A preliminary report on some experiments on bird migration. Condor **42:** 93–99.
79. Rowan, W. 1937. Effects of traffic disturbance and night illumination on London starlings. Nature **139:** 668–669.

THE STUDY OF WILD ANIMALS UNDER CONTROLLED CONDITIONS*

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In the course of studying taste discrimination in rats, Dr. Curt Richter gave some of his rats small amounts of alpha-naphtha-thio-urea. This substance, more simply designated ANTU, rather than proving to be a tool for studying taste discrimination, acted as a highly lethal poison.[1] Since it was so specific for rats (*Rattus norvegicus* only), it was thought that it might be a panacea for effectively eliminating this pest. With this as the stimulus, Johns Hopkins University and the City of Baltimore began a cooperative program on the control[2] and the study of the ecology of the Norway rat. Occasionally all the rats in a block were killed. More frequently, however, a small residual population remained, and from it Emlen *et al.*[3] found that there was a regrowth in less than a year to approximately the original population level, with different city blocks having different levels, which presumably reflects the "carrying capacity" of the area.

One of the problems we wished to answer was: "How is this limitation of population size brought about?" Predation pressure might be operative, but we have insufficient data on that point. In many blocks, the volume of food hardly appears to be a limiting factor since it is nearly continuously available in open garbage cans.

Two other possible factors limiting the population size are the distribution of availability of food and the distribution of availability of harborage sites. Whether or not they are limiting factors, they will operate at least to alter the frequency of contacts between individuals. The problem then arose as to how such an ecological behavior study might be conducted in the field. The field here was city blocks, where, due to human activity, the environment was less stable than with most animals. Ecologists are always plagued with the problem of determining which of several concomitantly operating variables is producing the observed changes in the organism studied. This is particularly true when studying the Norway rat.

Study of a Wild Rat Population

Therefore, it was decided to set up a pilot experiment, borrowing some of the techniques of laboratory sciences, in order to study the role of distribution of availability of food and harborage on the growth of a population of rats. FIGURE 1 gives details of the spatial relation of the pen in which five pairs of rats were introduced. The pen, which is 100 feet on a side, is surrounded by a barrier of electric fences and traps, which has effectively eliminated the factor of predation. Food as an influencing factor was reduced to the simplest possible situation by making it continuously available in a

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twenty-foot-square central pen. Harborage was constant and limited, in that no expansion was possible outside the 100-foot-square area surrounded by a rat-proof fence. Burrows might be dug anywhere or the nine sunken harborage boxes in each corner area might be used. Contacts between rats were more easily observed by limiting to four the passageways through the central food pen fence, and to four through the middle barrier fence. The rats were periodically trapped for examination, ear tagging, and pelage marking for observation from a tower.

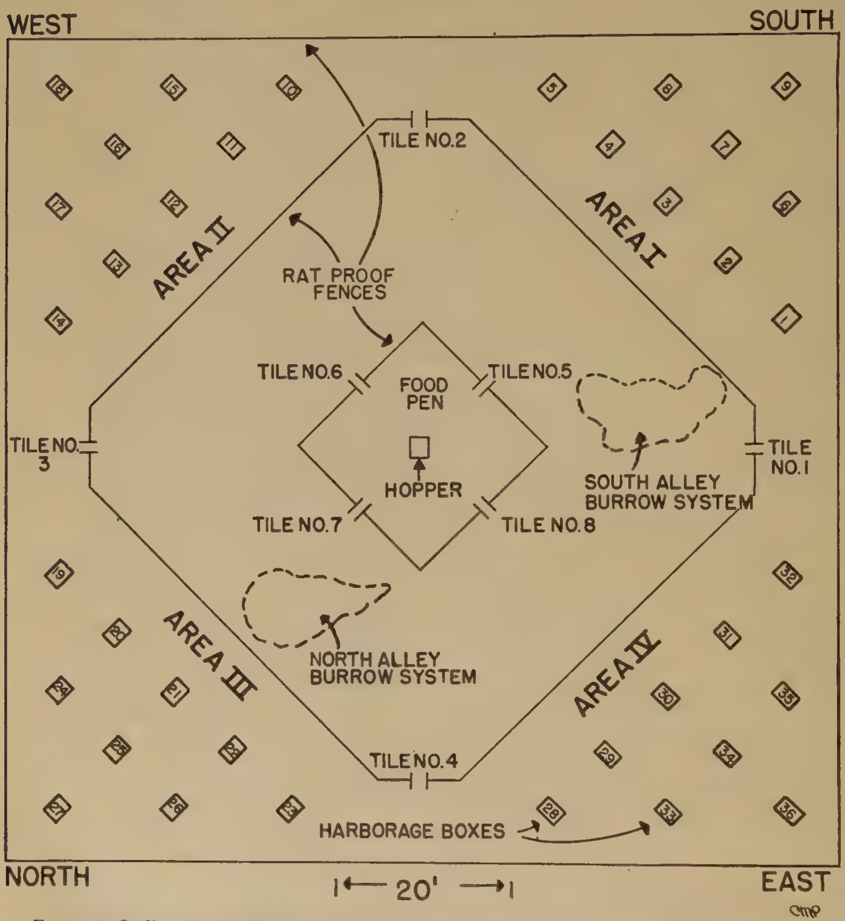

FIGURE 1. Outline of pen utilized in the study of behavior and population ecology of Norway rats.

This study has been under way for eighteen months. Final results will be published following its termination, after the population has reached a saturation point. However, the present data lead to several general conclusions, which will serve as my point of departure for outlining the need and scope of ecological and behavioristic studies of wild animals under such controlled conditions as approximate their natural habitat. These conclusions are:

(1) The arrangement of the pen was such as to produce a gradient of availability to the food. Rats living in the alleys adjoining the food pen were in a more favorable situation than those living in the four triangular areas.

(2) Rats born in the alleys grew more rapidly, and, since greater weight is a determining factor in attaining a high social rank in the hierarchy, they were favored in attaining high social status.

(3) Rats born in the triangular areas grew more slowly. Distance from the food became important, since, in getting to the food source, they made contact more frequently with adult rats. Social conditioning at such times is mainly by adults on juveniles, determining patterns which are retained as adults.

TABLE 1

PHYSICAL, PSYCHOLOGICAL, AND REPRODUCTIVE DIFFERENCES INDUCED BY AN ENVIRONMENTAL GRADIENT

(Data derived from January 1 to Sept. 25, 1948 observations)

		Av. wt. in gr.	*Av. no. of wounds*	*Number of pregnancies*	*Litters weaned*
Born in an area	♀ 17	379^7	14^6	3	1?
	♀ 20	388^4	14^4	4	0
	♀ 25	371^7	15^9	5	0
	L-3 ♀ ♀	379	14.3	12	1?
Born in alley	♀ 33	451^4	1^3	3	2 (3rd?)
	♀ 37	411^4	0.6^5	5	4
	♀ 43	426^4	3^4	4	4
	L-5 ♀ ♀	429	1.5	12	10

Litter 3 was born May 30, 1947 and Litter 5 August 16, 1947.
Superscripts denote numbers of observations from which averages were determined

(4) Social status may be passed to later generations. For example, smaller adults are forced into the peripheral, more unfavorable portions of the environment. Their young, because they are born there, grow more slowly and are thus also relegated to a low social status.

(5) There is less strife among rats which have been associated with each other during their development.

(6) Environment, particularly as it affects the pattern of contacts between rats, seems to be more important than heredity in determining the social status and the welfare of the individual.

In TABLE 1 are comparative data on females from two litters which reflect the impact of environmental gradients on this social species. From it, it may be noted that rats born in a suboptimal portion of the environment attained a lowered adult weight, were more frequently wounded in combat, and, though they conceived as often, rarely raised litters. These litters were born to two of the original females introduced in the pen. As adults, there was a 100 gram weight differential between these two mother rats. The heavier of these selected the alley as the site to rear her litter, while the lighter rat was forced into one of the triangular areas more distant from the food source.

These tentative conclusions in this pilot experiment will serve as a point of orientation for my remarks concerning the value and scope of studying population ecology under controlled conditions.

Providing an Optimum Environment

For every species, there must be a hypothetically optimum environment. Such an environment has reality only in relation to the attainment of the maximum welfare of the individual, which may be defined as the relative realization of the genetic limits to its physical, pyschological, and social potentialities. Whereas an individual may occasionally attain its maximum welfare, it is difficult to visualize all members of a population being so fortunate. Nevertheless, an optimum environment should provide the conditions in which a large number of individuals closely approximate the maximum individual welfare. This poses the problem of determining criteria for judging individual welfare. With the Norway rat, the growth curve or the weight at a given age may be used as such a criterion, since it reflects the social conditioning and the opportunities of the individual.

From our knowledge of the rat's requirements, the writer recently planned on paper what might be such an optimum environment for rats. In brief, the organization was for a system of adjoining sectors of a circle, the radii acting as partial barriers to dispersal of the rats to adjoining sectors. Food should be available in the apex of each sector. Peripheral to, and adjoining the food source, conditions should be made optimum for harborage. Just peripheral to the harborage area, a barrier should be placed with only a few passageways through it. Beyond this barrier, including the remaining portion of the sector, is what might be designated as a "wandering area." Rats exhibit a great deal of spontaneous activity or random wandering which must be necessary for their well being. By the introduction of the partial barrier between the harborage and the wandering areas, it should be possible to make a very abrupt transition between the two areas so that any rats forced to live in this latter area would find conditions particularly unfavorable, due to the fact that they would have to pass through passages defended by rats living on the other side, and would have to pass through the established colony in order to get food. That such a procedure might work in producing self-limitation of the population, while harming as few individuals as possible, is indicated by the fact that, in my pilot experiment, several rats living in such a situation, out in the triangular harborage areas, have been socially sterilized. Although some of these have had litters, none have been raised beyond the first few days. In regard to the portion of the sector assigned as a harborage area, it should be small enough to limit the colony to one where established relationships might develop among all individuals in a mature colony.

In a discussion of this plan for a theoretically optimum environment for rats, D. H. Calhoun informed me that the design was remarkably similar to that of the garden city concept[4, 5, 6] of planning of human communities. In essence, the garden city concept is of a limited small city surrounded by a greenbelt of agricultural and recreational areas (the wandering area postulated for rats) in which urban expansion is limited. Civic centers, stores, *etc.*, are located centrally (the feeding areas located at the apex of each sector postulated for rats). Radiating outward from the community oriented center of the garden city are super-blocks (the harborage portion of the sectors postulated for rats) several times the size of the usual city block. In these super-blocks, the focus of attention of the inhabitants is inward, so designed to foster closer local community integration. Perhaps this apparent similarity in the design of a hypothetical optimum environment for rats and the empirically determined optimum for man has no biological basis of comparison. Nevertheless, comparative studies seeking optimum conditions for the development of societies of different species of animals should contribute equally to the understanding of many problems confronting human welfare on the social level today, just as physiological studies on other animals in the past have advanced our control of human health problems.

If we are ever really to determine what optimum environments are, or if we are to understand the behavior of populations of many animals in nature, we must begin to attack the problems experimentally. Presumably, one of the first problems will be to segregate the two prime requirements which alter the behavior of populations, that is, food and shelter. Each of these must be viewed in relation to its effect on the reproductive behavior and the physical and psychological well-being of the individual. In their analysis, food and shelter may be broken down into gradient systems. Food gradients may be constructed to determine the effects of volume available or of the distribution of availability of food in space. Shelter is a more complicated problem. It involves harborage as such, home range or territoriality, and the physical configuration of the environment, which may alter contact rate, as well as escape from predation. Nevertheless, there is no reason why gradients of harborage availability, amount of space, or degree of forced contacts can not be set up in gradient systems. By so studying gradients of these environmental conditions, we can ascertain their role in the life of the species.

In FIGURE 2 is diagrammatically illustrated the type of experimental approach to studying these gradients. In addition to studying the effects of gradients of food and shelter, there should be the opportunity of bringing together individuals with different histories to determine the character of their interactions. This may be studied advantageously at the two extremes of the gradient systems. At one extreme, the populations may be brought in contact where food is continuously available. Here, only the character of individual contacts may be studied. Contacts at the other end of the gradient system may even be more revealing. Each pen forming the limits to the gradient system should be so designed as to allow the funneling off of the excess population into a vacuum environment where favorable conditions exist. In addition to the overflow from the gradient pens, there should be an overflow into the vacuum area from an area approaching optimum conditions. In this way, we could learn what types of individuals leave each set of environmental conditions, their fate as colonizers of a strange environment, and their interactions with animals of known but different history.

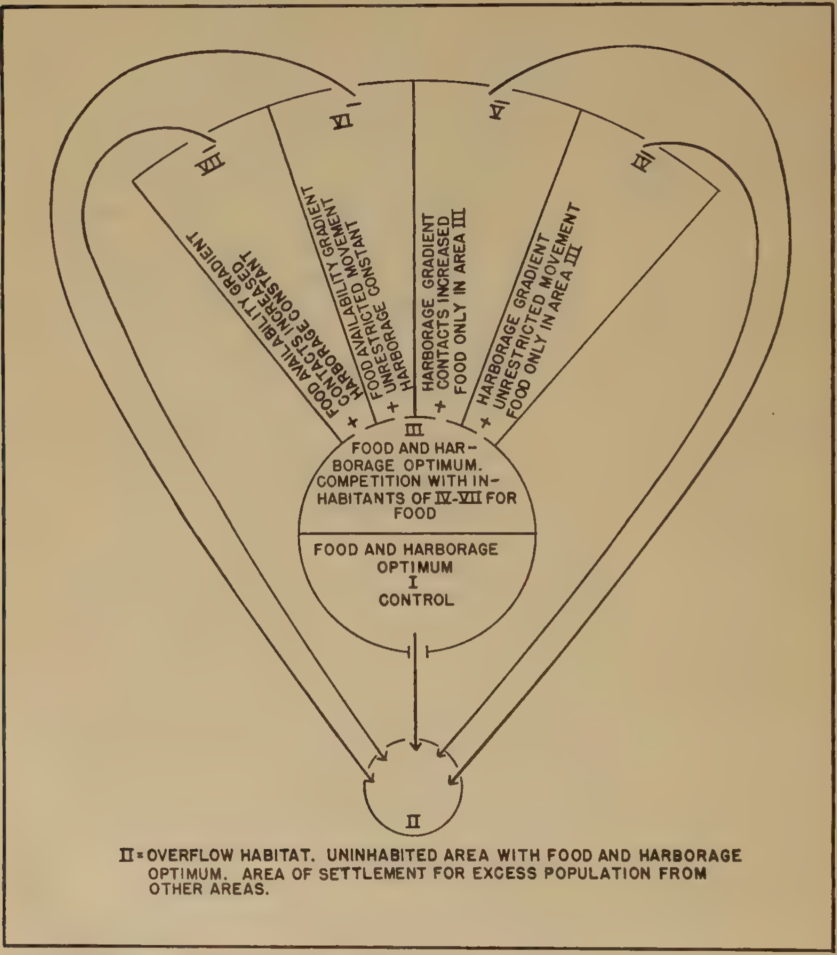
VII
VI
V
IV
FOOD AVAILABILITY GRADIENT
CONTACTS INCREASED
HARBORAGE CONSTANT
FOOD AVAILABILITY GRADIENT
UNRESTRICTED MOVEMENT
HARBORAGE CONSTANT
HARBORAGE GRADIENT
CONTACTS INCREASED
FOOD ONLY IN AREA III
HARBORAGE GRADIENT
UNRESTRICTED MOVEMENT
FOOD ONLY IN AREA III
+
+
+
+
III
FOOD AND HARBORAGE OPTIMUM. COMPETITION WITH INHABITANTS OF IV-VII FOR FOOD
FOOD AND HARBORAGE OPTIMUM
I
CONTROL
II
II = OVERFLOW HABITAT. UNINHABITED AREA WITH FOOD AND HARBORAGE OPTIMUM. AREA OF SETTLEMENT FOR EXCESS POPULATION FROM OTHER AREAS.

FIGURE 2. Diagram of technique for studying the effect of environmental gradients on behavior and population ecology. Size and shape of the compartments as well as the nature of the barriers between or within compartments will vary with the species and the problem. The lines terminating with arrows represent corridors connecting compartments.

Comparison of Mammalian Species Available for Population Studies

A knowledge of the factors controlling group behavior and physiology during stages of population growth will be interesting for its own sake, but its pursuit gains added importance in the light of human populations today. The populations of the United States, of other countries, and of the world itself are fast approaching, or have reached, the upper asymptote of their present logistic.[7, 8] It is at this level that behavior problems become most critical, both from the viewpoint of increased contacts, and the impact of limited space, shelter, or food supply. Ecologists frequently study populations living under natural conditions, but the interpretation of their observations is difficult because of the interplay of many simultaneously acting variables. For example, there is a voluminous literature on population cycles covering many animals.[9, 10] Yet, we still know essentially nothing concerning changes in behavior patterns during these cycles or of the factors which induce changes in physiology,[11] or rates of birth and death. We are simply at the descriptive stage of saying "cycles exist."

On the other hand, psychologists have developed a broad understanding of the individual. Working mainly with laboratory strains of the Norway rat, there has been a great host of experimentation on learning ability, motivation, discrimination, tropisms, *etc.*, but these have frequently had little relevance to the environment, to which their genetic constitution allows them to adjust. Nor do these experiments often take into consideration the fact that the rat is a social animal whose nature is modified by the social matrix in which it develops. Let it be understood that this is not an attempt to cast aspersion on the techniques of these two disciplines. Rather, it is an effort to point out that the time is now ripe for ecologists and psychologists to join hands in the analytical study of developmental population ecology.

On the invertebrate level, particularly with *Drosophila* and *Tribolium*, students of population dynamics have made considerable strides. Vertebrates, because of their greater development of sociality, on the level where it may be modified by environmental changes, pose a more difficult problem. The mere fact of requiring greater space for developing a natural society makes vertebrates more difficult to study than small insects, whose environment may be closely simulated in small glass containers. Even so, my studies on rats, penned under essentially normal conditions, convinces me that these difficulties are surmountable.

For the purpose of this discussion, the following remarks will be confined to mammals, since the knowledge of their ecology, physiology, psychology, and genetics is as advanced as in any other group of organisms.

In TABLE 2 are listed nine mammals most suited for the study of developmental population ecology. For each of fourteen characteristics, each species is weighed and their value given as zero or one to four pluses. These characteristics may be broken down into groups which will be discussed separately. It will be kept in mind that the evaluations are made with consideration of studying the animals under penned conditions, simulating natural conditions.

Group I is a variable group of characteristics which have important bearing on selecting an experimental animal with reference to all the other characteristics. Biotic potential is important for its relationship to the duration of an experiment. In this respect, the house mouse clearly has an advantage over dogs or chimpanzees. The factor of diurnality of the species is important with reference to man as the observer. Any strictly nocturnal species, such as *Peromyscus*, presents technical difficulties not encountered in highly diurnal animals, such as most ground squirrels. Observability has to do with size of the animal and its habits. Individuals must be marked for recognition. Despite a high reproductive rate and a small home range, *Microtus* is a poor experimental animal for many purposes because its subterranean habits and use of covered trailways make it difficult to observe. Smallness of home range is important in keeping as many individuals under observation as possible.

Group II has to do with the mechanics of the experimental set-up. Handling and the ease of repeated trapping is necessary for periodic examination of the reproductive and physical condition of individuals. By spatial relationships is meant the characteristics of home range, climbing ability, or harborage habits which determine the size of the pens, the ability to keep the animals within the pen, or to construct artificial harborage sites in which the animals may be observed or taken out for examination. It also includes the difficulties involved in altering contact rates by artificial barriers. The mechanical aspects of feeding requirements are viewed from the standpoint of studying gradients of availability. For example, localized sources of food might introduce unnatural situations among dogs and wolves, which are pack hunting animals, or among herbivorous mice, such as *Microtus*, whose normal food supply is also its cover.

TABLE 2

CHARACTERISTICS DESIRABLE IN ANIMALS USED FOR DEVELOPMENTAL POPULATION ECOLOGY

	Norway rat	*House mouse*	*Oryctolagus*	*Dog-wolf*	*Chimpanzee*	*Monkeys*	*Ground squirrels*	*Microtus*	*Peromyscus*
Biotic potential	+++	++++	++	+	0	+	++	+++	++
Diurnality	+	+	+	++	++++	++++	++++	++	0
Observability	++	+	+++	++++	++++	++++	++	0	+
Home range	+++	++++	++	+	+	+	+++	++++	+++
I Sub-total	9	10	8	8	9	10	11	9	6
Handling	+++	++++	+++	++	+	+	+++	++++	++++
Spatial relationships	+++	++++	+++	+	+	+	+++	++++	++
Feeding requirements	++++	++++	+++	+	+	++	++	+	+++
II Sub-total	10	12	9	4	3	4	8	9	9
Genetic strains	+++	++++	+++	++++	0	0	0	0	++
Physiological information	++++	+++	+++	+++	+	++	0	0	0
Psychological information	++++	++	0	+++	+++	+	0	0	0
III Sub-total	11	9	6	10	4	3	0	0	2
Food dependencies	+++	+	+	+++	++++	+++	++	+	+
Care of young	++	++	++	+++	++++	++++	+	+	++
Shelter dependencies	++++	++	++++	++	+	+	++++	+++	+
Reproductive attractions	+++	+++	+++	+	++++	+++	++	+++	++
IV Sub-total	12	8	10	9	13	11	9	8	6
Total	42	39	33	31	29	28	28	26	23

Group III encompasses sources of interpretive data and techniques for studying individuals with known social history. The availability of genetic strains is particularly important because it presents the opportunity for exposing different strains to similar environmental conditions, or different strains in competition, and thus revealing the relationship of heredity to social problems. This is but an elaboration of the extensive laboratory studies which, for example, have been made on competition among different strains of the house mouse.

Group IV encompasses what might be designated as social activators which keep the group together. In rating food dependencies, sharing food, formation of caches, and the mutual effort in procuring food must be considered. As a force for social adhesion, the period of dependency of young upon adults is important. Under shelter dependencies are included common effort in escaping enemies, development of communal harborage systems, and aggregations for warmth. Under reproductive attractions, the frequency of receptivity of the female and the duration of sexual potency of the male are paramount.

No doubt, many will disagree with my rating of some of the categories for some species, but the importance here is not in errors of evaluation, but in an approach in determining relative merits in selecting species for experimental studies in developmental population ecology. Depending upon the specific aims in view, one animal will have an advantage over another.

In 1930, Pearl[12] pointed out that the three primary biological variables in the growth of a population are natality, mortality, and migration and that social factors of various sorts, from a biological view, are secondary in nature, since they must operate on the former. Later, Pearl[8] remarked, concerning group behavior and psychology as social factors affecting growth, that "if there is any desire or intention to keep the investigation of population problems on a rigorously scientific footing, it seems wisest to leave aside for the present the discussion of psychological group attributes until some future time when they may perhaps become more precisely understood." In view of recent advances in field studies in population ecology, in group behavior, under the impetus of Allee and his students, and in the isolation of factors operating upon individual behavior by psychologists, it seems that science is now ready for a concerted attack on how these secondary factors influence the primary factors of population growth and, in turn, are influenced by them.

In such measure as this paper may have succeeded in pointing out one possible mode of attacking this problem, it is hoped that the writer may be pardoned for diverging so far afield from his own experimental results. Perhaps it may have helped to emphasize, for the field of social behavior, what Sinnott,[12] Lynd,[13] and Pearl[14] have previously done in other areas of biological research, that an analysis of the parts need not enlighten an understanding of the whole. The understanding of the individual, or of the group of which it is a part, must take into consideration the past, as well as current factors operating upon the population during its growth.

Summary

To study the biological properties of self-limitation of populations, a pilot experiment was initiated in which predation was eliminated from a population of rats living in a quarter-acre pen with abundant food. Control of

population size must then result from interactions among rats. Results to date form the basis for suggesting certain techniques for the study of social behavior as an aspect of population ecology. The results, in brief, are that rats born near the source of food grow more rapidly, and, conversely, those born distant from the food source grow more slowly; the latter, as a result of the fact that greater weight is a deciding factor in combat, are forced to remain in submarginal areas, and their young in turn tend to assume a low social status. Group continuity in space and time is of value in reducing strife. From such observations, the concept of an hypothetically optimum environment is forwarded. Experimental verification of optimum habitats must take into consideration individual and group welfare at the upper asymptote of the population growth curve, and must be attacked by studying gradients of availability of food and shelter as these are modified by spatial configurations of the environment. How these variables affect behavior, physiology, natality, mortality, and migration must be determined. Human populations are approaching their maximum growth. If studies in animal ecology and behavior are to have greatest relevance to the understanding of human social and psychological problems, we must study the factors affecting populations at different stages of their growth and apply techniques of physiological and psychological analysis, developed for the study of laboratory animals under essentially asocial conditions, to the study of individuals taken from a social group whose past history is known.

References

1. Emlen, J. T. 1947. Effectiveness of various rodenticides on populations of brown rats in Baltimore, Md. Amer. Jour. Hygiene **45:** 254–257.
2. Emlen, J. T. 1947. Baltimore's community rat control program. Amer. Jour. Pub. Health **37:** 721–727.
3. Emlen, J. T., A. W. Stokes, & C. P. Winsor. 1948. The rate of recovery of decimated populations of brown rats in nature. Ecology **29:** 133–145.
4. Violich, F. 1948. Planning for healthy cities. Ciba Symposia **9:** 877–892.
5. Mumford, L. 1938. The Culture of Cities. Harcourt, Brace and Co., New York.
6. Fulmer, O. K. Greenbelt. American Council on Public Affairs, 40 pp.
7. Pearl, R. 1930. The logistic curve and the census count of 1930. Science **72:** 1–2.
8. Pearl, R. 1937. On biological principles affecting populations: human and other. American Naturalist **71:** 50–68.
9. Dewey, E. R. & E. F. Dakin. 1947. Cycles: the Science of Prediction. Henry Holt and Co. New York.
10. Elton, C. S. 1942. Voles, Mice and Lemmings. The Clarendon Press. Oxford, England.
11. Green, R. G. & C. L. Larson. 1938. A description of shock disease in the snowshoe hare. Amer. Jour. Hyg. **28:** 190–212.
12. Pearl, R. 1930. Some aspects of the biology of human populations. E. V. Cowdry's Human Biology and Racial Welfare: 515–552.
13. Sinnott, E. W. 1939. The cell and the problem of organization. Science **89:** 41–48.
14. Lynd, R. S. 1939. Knowledge for What? Princeton Univ. Press. 268 pp.

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